

PROPELLER SCARRING IN A SEAGRASS ASSEMBLAGE: EFFECTS ON
SEAGRASS, PHYSICAL PROCESSES, AND RESPONSE OF ASSOCIATED
FAUNA

by
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Abstract

Damage to seagrasses by propeller scarring is common in coastal waters. Scarring has the potential to fragment seagrass beds resulting in habitat loss, decreased productivity, and the possibility for further erosion and degradation. A study was conducted in *Thalassia testudinum* beds in Puerto Rico to determine how seagrass plants, associated fauna, and physical processes are affected by this disturbance. Four treatments (propeller scar, seagrass/scar interface, and seagrass located 5 and 10 m from scars) were compared among 10 replicate seagrass beds. Scarring modified the faunal assemblage at the scale of the propeller-created gap; there was significantly lower total faunal abundance and fewer faunal species in scars. When individual taxa were considered, shrimp and mollusc abundances were significantly lower in scars. Resident fish abundance was not significantly different among treatments. Dominant shrimp species in scars differed from seagrass treatments. Crabs and molluscs responded negatively to scarring as indicated by significantly lower densities of these two taxa up to 5 m from scars. The extent to which these results “scale up” remains unknown and future studies should focus on larger, more intensely scarred areas.

Resumen

Las zanjas lineares en áreas de hierbas marinas causadas por las hélices de los motores son comunes en la costa donde el mar es poco profundo. Este tipo de disturbio tiene el potencial de fragmentar las praderas de hierbas marinas resultando en pérdida de hábitat, disminución en su productividad primaria y conllevan a su posterior erosión y degradación. El presente estudio se condujo en la costa sur-occidental de Puerto Rico para determinar cómo áreas de *Thalassia testudinum* y su fauna asociada se afectan por este disturbio antropogénico. Se analizaron cuatro diferentes tratamientos en diez sitios (en la zanja, en la interfase hierba/zanja, a 5 m de la zanja y a 10 m de la zanja). Las zanjas pueden modificar las comunidades de animales por la reducción en los números de especies y en la abundancia de fauna total y de los camarones y los moluscos en las zanjas. También, las poblaciones de camarones en las zanjas fueron diferentes a las adyacentes con hierbas en términos de las especies dominantes. Los cangrejos y los moluscos tuvieron baja densidad en los tratamientos de interfase y 5 m contra el tratamiento de 10 m. Se necesitan estudios a mayor escala donde este tipo de disturbio afecte áreas más grandes, o se presente con mayor frecuencia.

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1. INTRODUCTION

Disturbance is a fundamental component of ecosystem function and is a major influence on the spatial and temporal heterogeneity of ecosystems as well as the relative abundance of resident species. Disturbances are heterogeneous in time and space, and most commonly involve the modification of or removal of habitat structural components, with subsequent alterations to the usual physical and biological processes taking place within the disturbed ecosystem (Sousa, 1979; White and Pickett, 1985; Forman, 1995). Disturbance events fashion ecosystems that are composed of mosaics of habitat patches of varying shape and size (Sousa, 1979; Forman and Godron, 1981).

In most cases, the primary effect of a disturbance is the formation of a gap, in which a space, devoid of some form of structure or biomass, is opened by the disturbance. The gap is still surrounded by structural elements and is smaller than the area of continuous occupied substratum (Type I gap; Sousa, 1985). The formation of gaps has been documented in numerous systems ranging from temperate forests and grasslands, to the rocky intertidal, coral reefs and seagrass beds (Patriquin, 1975; Connell and Keough, 1985; Hobbs and Mooney, 1985; Runkle, 1985; Sousa, 1985). Frequent or prolonged disturbances within a system can lead to the formation of numerous gaps and ultimately fragmentation. Fragmentation of native habitat is one of the major reasons for decreases in world biodiversity (Wilcox and Murphy, 1985; Majer et al., 1997). Whether interior portions of habitat are physically removed or the intact habitat is fractured into remnant patches, the amount of edge and edge-

like habitat within the ecosystem is increased. Lovejoy et al. (1986) saw edge effects as the leading factor promoting ecological changes resulting from habitat fragmentation.

The concept of edge and edge effect is not new to ecology (Gleason, 1926; Leopold, 1933; Odum, 1971). Edge refers to the outer portion of a landscape element (near the perimeter), often defined by the junction between two different ecosystems resulting in the formation of a transition zone, or ecotone (Odum, 1971; Forman, 1995). Distinct environmental conditions occur at edges that are distinguishable from the interior of the habitat (Williams-Linera, 1990; Kapos et al., 1993; Matlack, 1993; Young and Mitchell, 1994; Stevens and Husband, 1998). Traditionally, edge effect refers to the tendency for increased species numbers and diversity at habitat edges versus habitat core (Odum, 1971). These increases are often attributed to the fact that the edge contains structural components from both systems, and therefore increases in abundance and diversity result from the mixing of populations from both communities. This phenomenon has been observed in a variety of aquatic and terrestrial systems (Peterson and Turner, 1994; Downie et al., 1996; Bologna, 1998). However, there are also some edge studies in which either no edge effect is apparent or species richness and diversity decline at the edge (King et al., 1997; Kruger and Lawes, 1997; Ozanne et al., 1997; Stevens and Husband, 1998). Interestingly, the edges examined in these studies were “hard” edges that did not exhibit the typical gradation of one ecosystem or habitat into another. Such edges are common in fragmented landscapes and tend to be artificial edges created by

rapid anthropogenic disturbances such as fire, grazing, or human activities (Lovejoy et al., 1986; Kruger and Lawes, 1997).

In addition to modifying faunal communities via the direct removal of structure, fragmentation alters physical processes occurring at edges thereby compounding actual habitat loss (Saunders et al., 1991). Fragmentation has been shown to modify nutrient cycles, radiation balance, wind profiles, local hydrologic cycles, and vegetation composition (Saunders et al., 1991).

The effects of habitat fragmentation, especially the formation of edges and remnant patches, is of utmost importance for terrestrial conservation biologists, especially in regard to the formation and designation of reserves and protected areas (Wilcox and Murphy, 1985; Saunders et al., 1991; Gascon et al., 2000). For example, until recently, the extent of edge effects due to fragmentation has been viewed as being controlled by some fixed distance from the edge. Gascon et al. (2000) suggest that anthropogenic edges, and their subsequent effects, may actually encroach further into a remnant patch, if the habitat surrounding the remnant is not conducive to regeneration or is conducive to further disturbance. In time, the remnant may become entirely composed of edge habitat. This issue is critical for reserve design. If the edges of reserves are not protected or if the habitat surrounding the reserve is too harsh, the reserve may collapse over time (Gascon et al., 2000).

Fragmentation is not limited to terrestrial communities. In the tropical marine environment, fragmentation has been documented in coral reefs, mangroves, and seagrass beds (Wilson, 1949; Harmelin-Vivien and Laboute,

1986; Dollar and Tribble, 1993; Sargent et al., 1994; Strong and Bancroft, 1994; Hastings et al., 1995; Riegl and Riegl, 1996). Seagrass beds in particular furnish a marine analog to terrestrial ecosystems such as grasslands, and may serve as an ecological model system for concepts currently under investigation in terrestrial landscape ecology, especially effects from fragmentation (McNeill and Fairweather, 1993; Robbins and Bell, 1994; Irlandi et al., 1995).

One of the most common disturbances to seagrass beds is the formation of propeller scars. Scarring occurs when a boat enters an area where the water is shallower than the depth of the boat's propeller. Initially, the upright seagrass blades are cut off by the slicing action of the propeller. As the boat proceeds and water depth decreases further, the propeller can tear into short shoots (erect stems that produce foliage leaves), sediment, and underlying rhizomes (horizontal stems embedded in substrate). When the propeller penetrates the sediment, a long, narrow gap, or prop scar, is created in which seagrass density and biomass are severely reduced or completely removed.

Seagrass beds are dominant features along shallow-water coastal marine environments and have been shown to be highly productive. High faunal diversity is maintained through several trophic levels, because the beds function as habitats, nurseries, feeding grounds, settlement sites, and refuge areas for a large number of ecologically and commercially important marine organisms (Zieman, 1982; Phillips, 1984; Thayer and Fonseca, 1984; Zieman and Zieman, 1989; Gotceitas et al., 1997). Several studies provide evidence that faunal densities and species diversity are lower on bare substrates than adjacent

seagrass beds (O'Gower and Wacasey, 1967; Santos and Simon, 1974; Thayer et al., 1975; Thorhaug and Roessler, 1977; Stoner, 1980a, 1983a; Homziak et al., 1982; Virnstein et al., 1983; Lewis, 1984; Orth et al., 1984; Wells et al., 1985; Carpenter and Lodge, 1986; Edgar, 1990; Edgar et al., 1994; Connolly, 1997; Jenkins and Sutherland, 1997; but see Young and Young, 1982). In addition to direct removal of structure, propeller scarring leads to a decline in productivity (Fonseca, 1994) and can increase sediment resuspension, and facilitate erosion by waves and currents (Fonseca, 1994). Fragmentation of large portions of seagrass beds could lead to a cumulative reduction in remaining viable habitat for fauna.

Few studies have directly addressed the importance of seagrass edges and fragmentation as a conservation issue (Orth, 1975; McNeill and Fairweather, 1993; Irlandi, et al., 1995; Lovegrove, 1997; Frost et al., 1999), even though such studies would provide pertinent information to managers when selecting sites for restoration and preservation. Because of the direct loss of habitat, it is often assumed that propeller scarring has a detrimental affect on seagrass communities but to date, no studies have assessed the effects of this type of disturbance on fauna. Results from natural seagrass edge studies (e.g. Bologna, 1998) are not directly applicable to anthropogenic edges such as those formed by propeller scarring. Scarring is a unique process in which narrow, linear gaps are created within a continuous grass bed. Are these gaps and their associated edges large enough to be perceived and responded to by fauna?

The first objective of this study was to characterize seagrass assemblages bordering propeller scars.

Faunal species numbers and abundances increase with increasing seagrass biomass and density (Orth, 1973, 1977; Heck and Wetstone, 1977; Brook, 1978; Heck and Orth, 1980; Stoner, 1980a, 1980b, 1983b; Lewis, 1984; Stoner and Lewis, 1985; Bell and Westoby, 1986). Differences in faunal densities should therefore correspond to differences in seagrass biomass and density resulting from propeller scarring. Seagrass biomass and density have been shown to be greater in interior portions of seagrass beds than in natural bed edges (Zieman, 1972; Orth, 1977; Thayer and Fonseca, 1984; Duarte and Sand-Jensen, 1990; Bologna, 1998; Nakaoka and Aioi, 1999). A second objective of this study was to determine if seagrass biomass, density, and leaf area index differ at the edges of scars versus bed interiors and if so, do faunal abundances reflect these differences?

In temperate and tropical forests, edges can significantly differ from the forest interior in terms of light penetration, temperature, humidity, and wind speed (Williams-Linera, 1990; Kapos et al., 1993; Matlack, 1993; Young and Mitchell, 1994; Stevens and Husband, 1998). Sediment composition and water velocity are similarly affected along seagrass meadow edges (Orth, 1977; Fonseca et al., 1982). Seagrass beds are effective sediment traps and tend to accumulate finer particles than unvegetated areas (Orth, 1977). Seagrasses also reduce current velocity at bed edges (Fonseca et al., 1982); the immediate decline in flow at bed edges causes larger particles to fall from the water column,

whereas fines are transported further into the bed, leading to a concentration of fine particles in bed interiors. Substrate composition influences various shrimp taxa, benthic infauna, and Pacific flatfishes (Williams, 1958; Ruello, 1973; Rulifson, 1981; Moles and Norcross, 1995; Seiderer and Newell, 1999 and references therein; Pinedo et al., 2000). Additionally, water velocity may influence the distribution of aquatic animals, especially larvae (Butman, 1987; Bologna and Heck, 2000), and currents have been shown to play a role in the distribution of adult forms, for example, holothurians and certain molluscs (Warwick and Uncles, 1980; Barkai, 1991; Levinton et al., 1995; Sakurai and Seto, 2000). A third objective of this study was to determine differences (if any) in sediment grain size and relative water motion among treatments scar, edge, and seagrass interior treatments.

This study evaluates the potential impacts of propeller scars to Puerto Rican seagrass meadows, focusing on impacts to seagrass plants, seagrass-associated fauna, and certain physical processes occurring in seagrass beds. The following null hypotheses were tested: 1) no difference in seagrass density, biomass, and leaf area index among propeller scars, seagrass edges directly adjacent to scars, and seagrass bed interiors at distances of 5 and 10 m from scars; 2) no difference in relative water movement and sediment composition among scar, edge, and seagrass interiors; 3) no difference in the abundance and composition of associated fauna among scar, edge, and seagrass interiors.

2. METHODS

This study was conducted between the months of May and November 1999 off the southwest coast of Puerto Rico near La Parguera (17° 58' N, 67° 03' W, Figure 1). The area consists of a number of inshore and offshore coral reefs, scattered mangrove islands, and seagrass beds within the inner insular shelf. The dominant seagrass species is *Thalassia testudinum*, but beds may be interspersed with *Halodule wrightii* and/or *Syringodium filiforme*.

Ten seagrass beds were chosen based upon level of scarring and amount of contiguous seagrass within the bed. Each site contained a single propeller scar that was bordered on all sides by at least 20 m of continuous seagrass. Scars were readily recognizable as recent injuries, with no signs of additional erosion beyond that of the original scar path. Scars were at least 3 m in length and 0.25 m in width. Four treatments were distinguished per site: propeller scar (bare sand trench resulting from prop dredging), edge (seagrass within 0.25 m of the scar), 5 m interior (distance of 5 m from the scar), and 10 m interior (distance of 10 m from the scar). The scars were measured for length and divided into 10 equal-length sections, each marked with a piece of surveyor's tape attached to a galvanized nail. The sections were marked in this way for ease of visibility from above the surface of the water as an aid for drop trap placement. Sections were marked in the same manner within the seagrass edge, 5 m, and 10 m treatments. Three different sections from within each treatment (scar, edge, 5 m, 10 m) were randomly chosen for clod card placement, sediment extractions, and

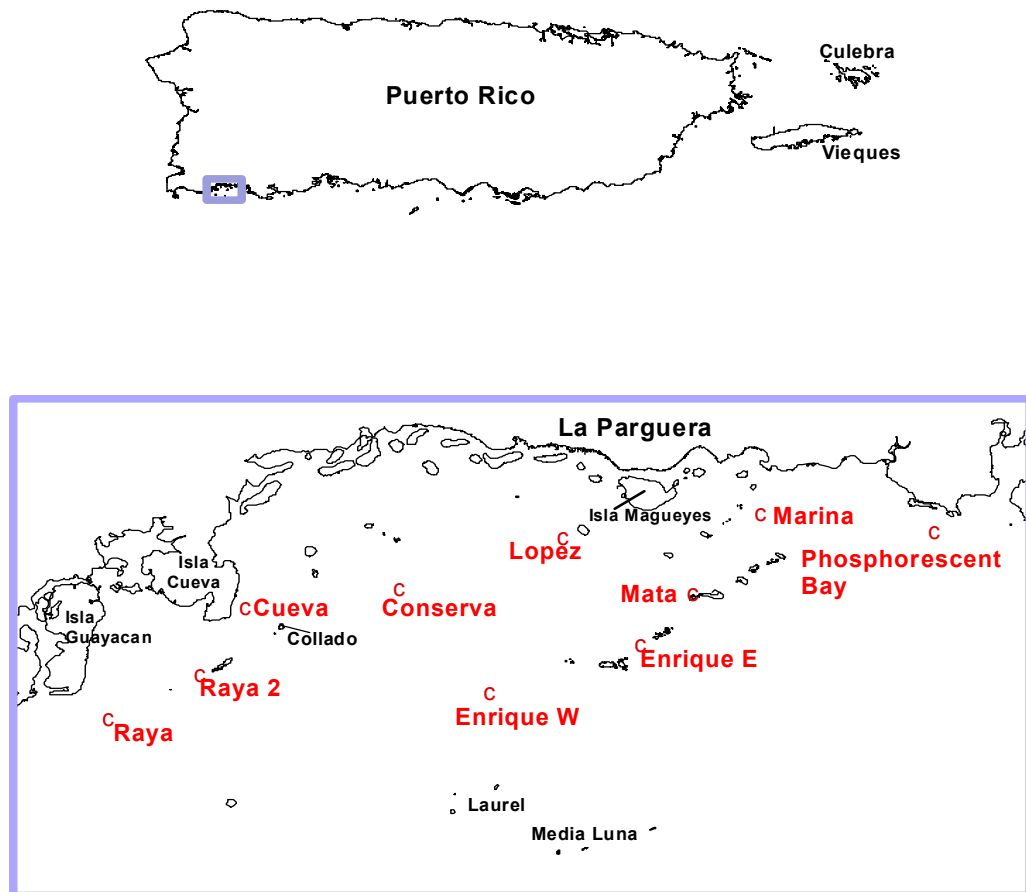


Figure 1. Map of the shoreline and associated reefs near La Parguera, Puerto Rico. Red flags indicate the ten study sites chosen for this project.

seagrass and faunal sampling (Figure 2). Clod card procedures and sediment extractions occurred prior to faunal sampling. A single site was sampled completely before moving on to the next site, and an entire compliment of samples from within a site was completed within 10 days.

2.a. *Flow*

Within each treatment, relative amounts of flow were recorded using clod cards (Doty, 1971; Thompson and Glenn, 1994). This method relates water flow to the dissolution rate (grams lost per unit time) of plaster of Paris (calcium sulfate) clods. All clods were made from the same batch of plaster of Paris to avoid inconsistencies due to differences in water or calcium sulfate content of the plaster mixture. The plaster mixture consisted of 7000 g reagent-grade plaster slowly added to 4690 ml water (Thompson and Glenn, 1994). The mixture was poured into oblong, round-bottomed polyethylene ice-cube trays. After 20 min, the clods were removed from the tray, and the flat ends of each clod were filed so that clod weights ranged from 27.04 to 30.04 g. Clods were < 3.0 cm in height. Clods were dried for four days and then cemented to thin, clear plastic cards using contact cement. The completed cards were then allowed to dry for another 24 h. After drying, the cards were weighed to the nearest 0.1 g. Three replicate cards were placed within each treatment within the selected sections (Figure 2). Cards were secured with galvanized nails and remained in situ for 48 h. The cards were then removed from the sites, rinsed with distilled water, and allowed to dry for four days in the laboratory. After drying, the cards were

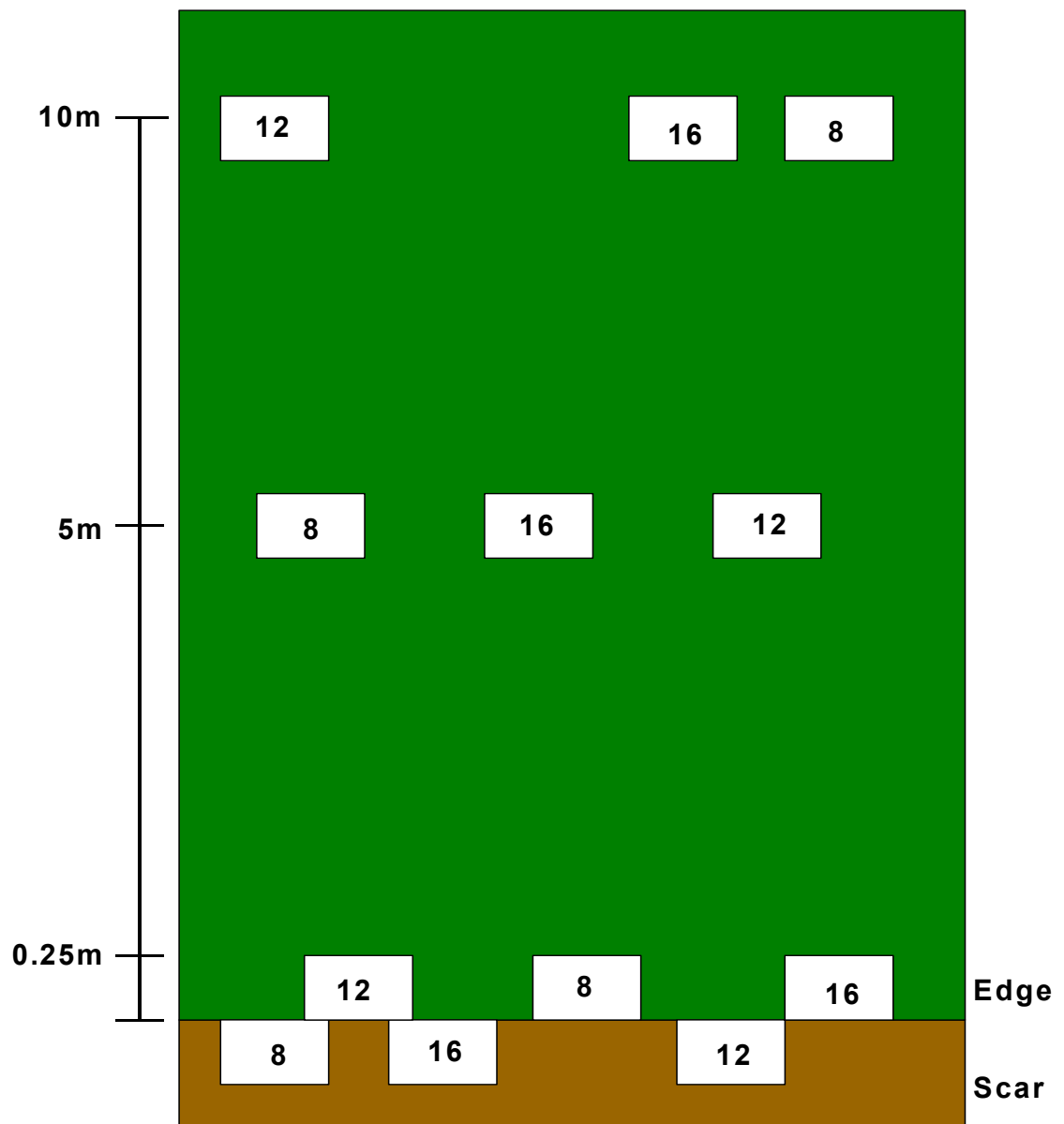


Figure 2. Schematic diagram of the experimental design used in the study. White boxes represent random sections within each treatment. Numbers within the boxes are the time of day that sampling occurred (e.g. “8” represents 0800 h etc.).

weighed, and the amount of plaster dissolved was calculated to the nearest 0.1 g. This method does not yield exact flow rates (Doty, 1971; Thompson and Glenn, 1994) but is a useful tool for comparing relative flow among different field sites.

2.b *Sediment*

Sediment samples were taken and analyzed following the procedure of Folk (1974). A 28 mm diameter plastic centrifuge tube with the tip removed served as a sediment core. Three sediment samples were taken from within each treatment at randomly selected sections (one sample per section) by pushing the open-ended tube approximately 5 cm into the sediment. The tube was then capped, removed from the substrate, and the sample was placed in a glass specimen jar. Large detritus particles were removed and excess water decanted. Samples consisted of approximately 20 g of sediment and were treated with 20 % hydrogen peroxide for 24 h to dissolve organics, dried at 60 °C and then weighed to yield total sample weight. Samples were then wet-sieved, retaining two fractions: gravel, > 2 mm, and sand, 0.0625 mm - 2.0 mm. Sand and gravel portions were dried (60 °C for 24 h), weighed, and the weight of the fine portion determined by subtraction. Percent composition for each fraction was then calculated.

2.c. *Fauna*

Seagrass fauna were sampled using a drop trap as modified from Holmquist's throw trap (1997). Throw traps have proven to be highly efficient and are the recommended method for faunal surveys in subtidal unvegetated

habitats as well as seagrass (Rozas and Minello, 1997). The trap used in this study is a 0.25 x 0.25 m open-ended box constructed of sheet aluminum with a depth of 0.4 m. Three random sections from within each treatment were selected for sampling with the restriction that there was a minimum of a two-section distance between samples taken from adjacent treatments. Sampling times of 0800, 1200, and 1600 were randomly assigned to each of three sampling days, and fieldwork was conducted such that there was a minimum of 24 h between samplings. On each day, one section from within each treatment was trapped (Figure 2).

Because the trap was to be manually placed into the substrate rather than thrown, a mechanism was devised to allow for distance between the sampler and the sampled treatment. Vise-grip panel clamps were used to grip one of the top edges of the trap. A five-foot long, two-inch diameter PVC tube was fitted over the handles of the pliers to act as an extension. The trap was then hoisted from the boat by the sampler, placed on the substrate, and pushed into the sediment approximately 1 to 2 cm. The trap was held in place with lead weights suspended from the trap corners. Fauna were cleared from the trap by passing a 0.25 m wide, handled net through the trap at the water/sediment interface. The net was emptied of its contents into a 19 L plastic bucket filled with seawater. Ten net passes were made in each trap. Buckets were then transported to the laboratory where fauna were sorted live, enumerated, and identified using the following groups: shrimps, fishes, crabs, and molluscs. These taxa were chosen based upon their common occurrence in seagrass beds, and the ease with which

they can be captured using the above methodology. Where possible, individuals were identified to species, with the exception of crabs which were separated into Brachyura and Anomura. Total faunal abundance and abundances within each group were determined and scaled to per m^2 values. Total number of species per 0.25 m^2 trap was calculated. Shrimp species comprising less than 9 % of the total number of individuals collected were pooled. Molluscs and fishes were treated similarly.

2.d. *Seagrass*

Seagrass sampling occurred after throw trapping in those treatments where seagrass was present (i.e., edge, 5 m interior, 10 m interior). Replicate quadrats ($0.125 \times 0.125 \text{ m}$) were haphazardly placed in the grass, and all seagrass short shoots within the quadrats were removed, placed in plastic bags, and transported to the laboratory for analysis.

In the laboratory, short shoot counts were made to determine short shoot density. Five short shoots were selected at random, and the number of blades per short shoot and the length and width of each blade were measured to calculate leaf area index (L. A. I. = mean blade length x mean blade width x mean number of blades per short shoot x mean number of short shoots per square meter x 2). The green, photosynthetic portions of all blades collected were washed in dilute HCl and gently scraped to remove carbonate epiphytes and sediment then dried at 90°C for 24 h to determine above ground standing crop per m^2 (dry biomass).

2.e. *Data Analysis*

Scar-edge, scar-5 m, scar-10 m, edge-5 m, edge-10 m, and 5 m-10 m were contrasted for vegetation parameters, sediment grain size, clod card weight loss, total faunal abundance, number of species, and abundances of various taxa. Untransformed mean values with standard errors are also reported because these values are more intuitive and provide additional perspective; although, probabilities generated from the aforementioned contrasts cannot be directly inferred from inspection of means with standard errors. Normality was tested using the Shapiro-Wilk test (Shapiro and Wilk, 1965). Bartlett's Test and the F-max test (Hartley, 1950) were used to test for homogeneity of variances. Where necessary, data were either log or square root transformed to meet the assumptions (Table 1). Where data met the assumptions, paired t-tests (two-tailed) were used. For data not meeting the assumptions, non-parametric Wilcoxon Sign Rank tests were used. The sequential Bonferroni method was used to reduce multiple comparison testing error (Holm, 1979). Rank-abundance plots were constructed as a representation of community diversity. A two-way ANOVA was used to test for the interaction between treatment and taxa. All statistical analyses were performed using SAS Version 8.0 (SAS Institute, Inc., 1999).

Table 1. Transformations and statistical tests used for each variable. N/A = transformation not necessary

Parameter	Test	Transformation
Clod Card Weight Loss	Paired t-test (two-tail)	N/A
% Sand	Paired t-test (two-tail)	N/A
% Gravel	Paired t-test (two-tail)	N/A
% Fines	Paired t-test (two-tail)	N/A
Seagrass Biomass	Paired t-test (two-tail)	N/A
Seagrass Density	Paired t-test (two-tail)	N/A
Seagrass Leaf Area Index	Paired t-test (two-tail)	N/A
Treatment x Taxa	2-Way ANOVA	Log (y + 1)
Total # Species	Paired t-test (two-tail)	N/A
Total Fauna	Paired t-test (two-tail)	Square root (y+ 0.5)
Total Shrimps	Paired t-test (two-tail)	Square root (y+ 0.5)
<i>Thor manningi</i>	Paired t-test (two-tail)	Log (y+ 1)
<i>Hippolyte zostericola/pleuracanthus</i>	Paired t-test (two-tail)	Log (y+ 1)
<i>Alpheus normanni</i>	Paired t-test (two-tail)	N/A
<i>Periclimenes americanus</i>	Paired t-test (two-tail)	Log (y+ 1)
<i>Latreutes fucorum</i>	Paired t-test (two-tail)	Log (y+ 1)
Pooled Shrimps	Paired t-test (two-tail)	Log (y+ 1)
Total Fishes	Paired t-test (two-tail)	N/A

Table 1. Con't.

Parameter	Test	Transformation
<i>Malacotenus macropus</i>	Wilcoxon Sign Rank	N/A
<i>Bathygobius curacao</i>	Wilcoxon Sign Rank	N/A
Pooled Fishes	Wilcoxon Sign Rank	N/A
Total Crabs	Paired t-test (two-tail)	N/A
Brachyurans	Paired t-test (two-tail)	N/A
Anomurans	Paired t-test (two-tail)	Log (y+ 1)
Total Molluscs	Paired t-test (two-tail)	Log (y+ 1)
<i>Cerithium eberneum</i>	Paired t-test (two-tail)	Log (y+ 1)
<i>Cerithiopsis greenii</i>	Paired t-test (two-tail)	Log (y+ 1)
<i>Tricolia bella</i>	Paired t-test (two-tail)	Log (y+ 1)
<i>Modulus modulus</i>	Paired t-test (two-tail)	Log (y+ 1)
Pooled Molluscs	Paired t-test (two-tail)	Log (y+ 1)

3. RESULTS

3.a. *Flow*

Mean clod card weight loss was greatest in the edge treatment (Table 2). Dissolution rates of the clod cards were significantly greater in the edge treatment relative to the scar, 5 m, and 10 m treatments (Table 3, Figure 3). No other contrasts were significant (Table 3, Figure 3).

3.b. *Sediment*

Sand was the dominant sediment grain size in each of the four treatments (Table 2, Figure 4). Percent sand content was significantly lower in scars versus the other treatments (Table 3, Figure 5). The percent composition of gravel ranged from 5.2 – 14.4 % (Table 2, Figure 6). Gravel content was significantly higher in the scars versus the edge, 5 m, and 10 m treatments (Table 3, Figure 6). There were no significant differences among treatments when contrasted for percent fines (Table 3, Figure 7).

3.c. *Seagrass*

The lack of seagrass in scars (i.e. zero values for all seagrass parameters), prevented direct comparison with the vegetated treatments. However, by definition, comparisons of scars to vegetated treatments would be significantly different. Seagrass parameters were similar among those treatments having seagrass (Table 2). Standing crop, short shoot density, and leaf area index exhibited no significant differences among vegetated treatments (Table 3, Figures 8, 9, and 10).

Table 2. Means (S. E.) for clod cards, sediment, seagrass, total fauna, and total number of species within each treatment (N = 10).

Parameter	scar	edge	5m	10m
Clod Card Weight Loss (g)	17.4 (1.5)	19.4 (1.4)	17.8 (1.4)	17.3 (1.5)
% Sand	75.3 (3.4)	81.6 (1.6)	83.3 (2.3)	82.7 (2.3)
% Gravel	14.4 (3.2)	6.3 (2.0)	5.2 (1.4)	5.4 (1.6)
% Fines	10.4 (1.6)	12.1 (1.2)	11.4 (1.3)	11.9 (1.7)
Standing Crop (g / m ²)	0 (0)	35.3 (6.1)	35.3 (6.1)	34.8 (4.1)
Short Shoots / m ²	0 (0)	1661 (94.3)	1566 (76.9)	1454 (110.1)
Leaf Area Index (m ² / m ²)	0 (0)	6.2 (1.0)	5.6 (1.0)	6.0 (0.7)
Total Fauna / m ²	67.7 (18.3)	200.0 (41.1)	203.2 (43.5)	283.2 (23.8)
Total # Species / 0.25 m ²	1.6 (0.3)	5.0 (0.7)	5.2 (0.7)	6.2 (0.5)

Table 3. P-values resulting from paired, two-tailed t-tests comparing differences in mean clod card weight loss, sediment composition, seagrass parameters, total fauna, and total number of species between pairs of treatments. *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons; N/A = insufficient data to run analysis

Variable	scar-- edge	scar-- 5m	scar-- 10m	edge-- 5m	edge-- 10m	5m-- 10m
Clod Card Weight Loss (g)	0.004**	0.463	0.869	0.002**	0.018*	0.290
% Sand	0.013*	0.012*	0.025*	0.373	0.528	0.687
% Gravel	0.002**	0.010**	0.0264*	0.620	0.684	0.917
% Fines	0.054	0.221	0.212	0.421	0.867	0.502
Standing Crop (g / m ²)	N/A	N/A	N/A	0.997	0.877	0.889
Short Shoots / m ²	N/A	N/A	N/A	0.325	0.112	0.102
Leaf Area Index (m ² / m ²)	N/A	N/A	N/A	0.264	0.533	0.746
Total Fauna / m ²	<0.0001**	<0.0001**	<0.0001**	0.965	0.002**	0.004**
Total # Species / m ²	0.0004**	0.0001**	<0.0001**	0.602	0.135	0.203

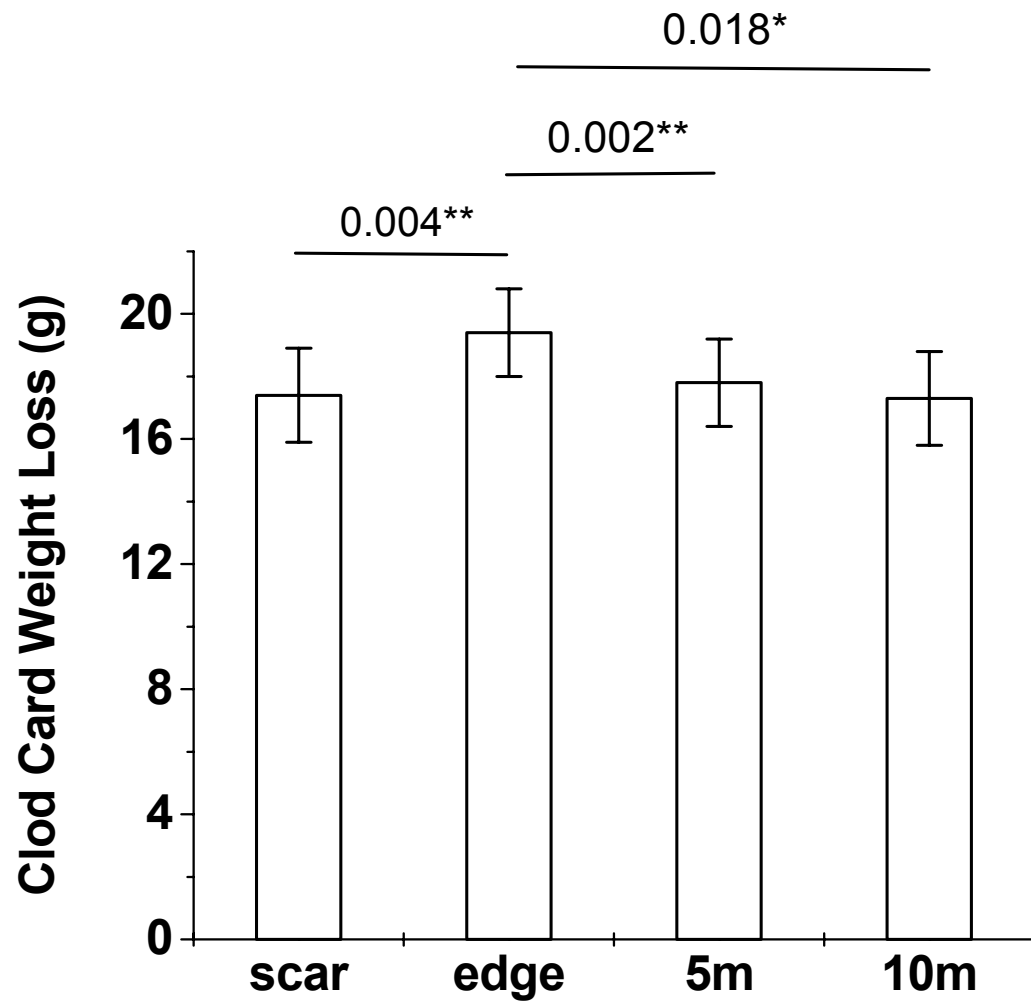


Figure 3. Mean (S. E.) clod card weight loss (g) within each treatment (N = 10). *significant at the per-contrast error rate ($\alpha = 0.05$); **significant after correcting for multiple comparisons

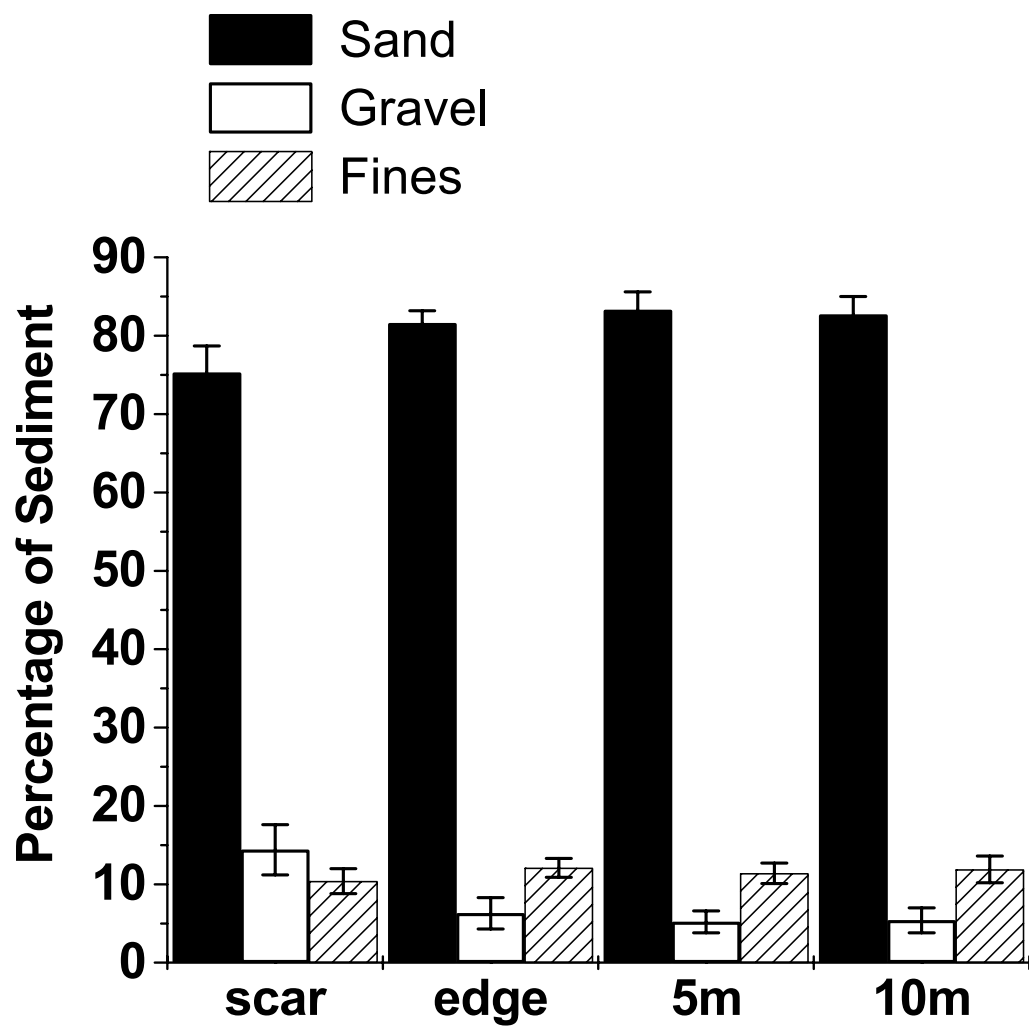


Figure 4. Mean (S. E.) percent composition of sand, gravel, and fines across all treatments (N = 10).

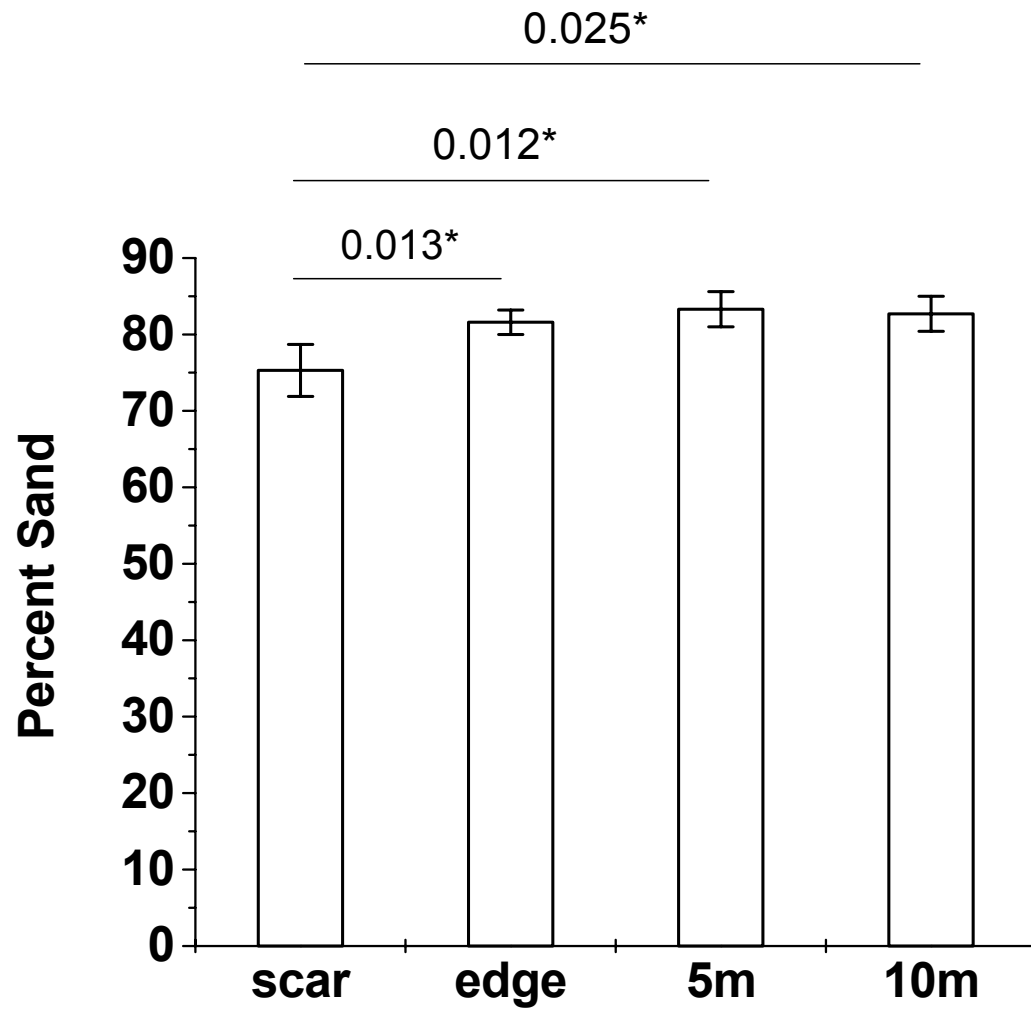


Figure 5. Mean (S. E.) percent composition of sand across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05)

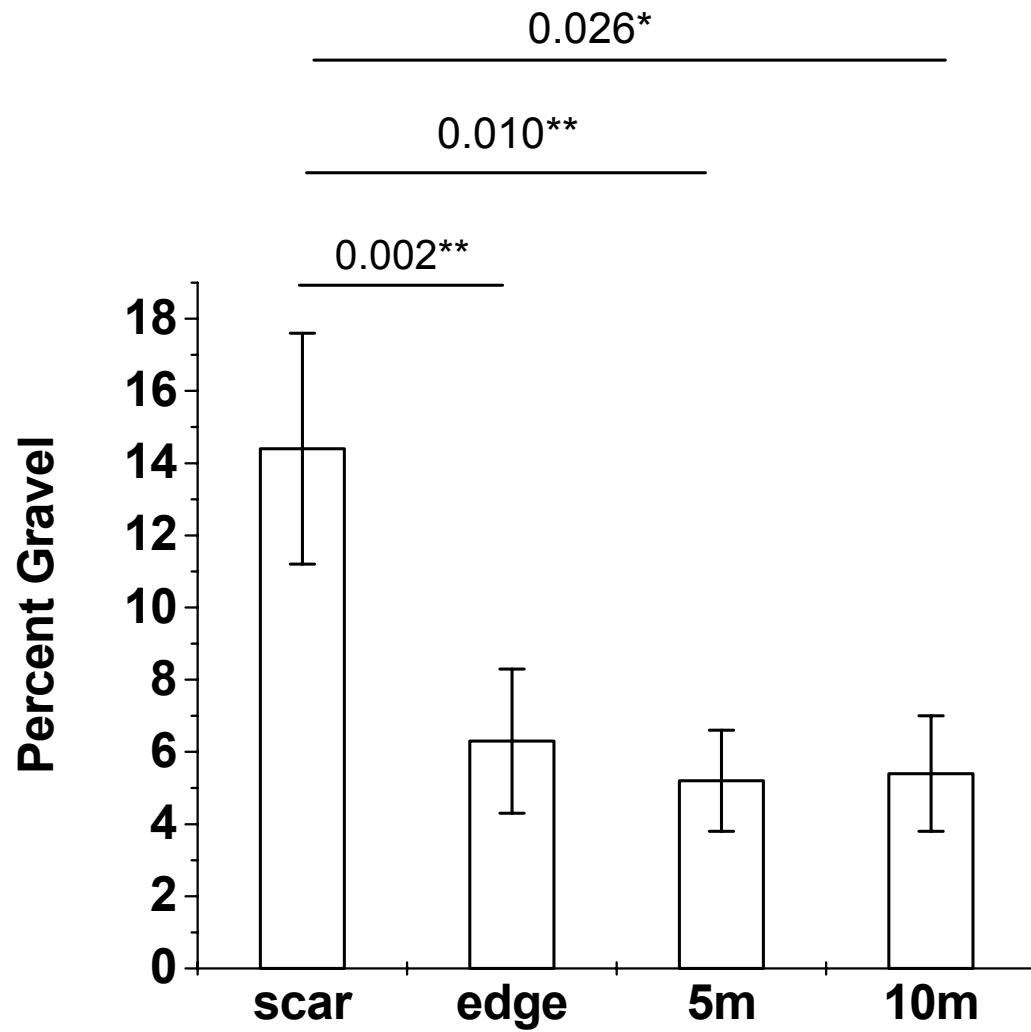


Figure 6. Mean (S. E.) percent composition of gravel across all treatments (N = 10). *significant at the per-contrast error rate ($\alpha = 0.05$); **significant after correcting for multiple comparisons

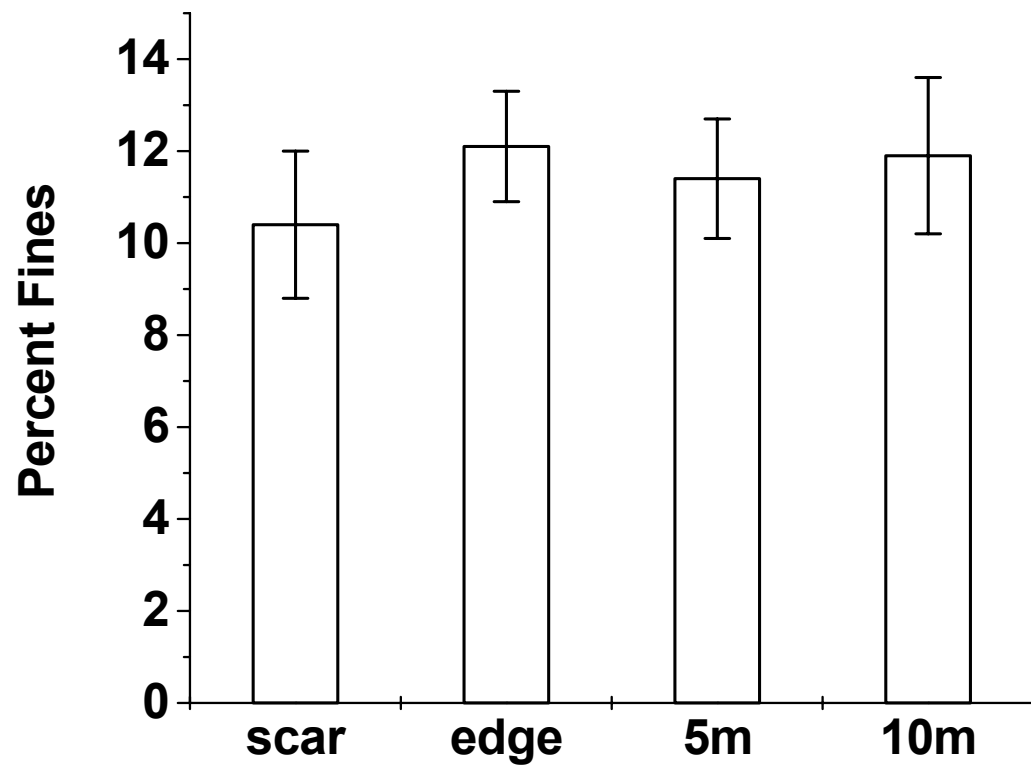


Figure 7. Mean (S. E.) percent composition of fines across all treatments (N = 10). No contrasts were significant.

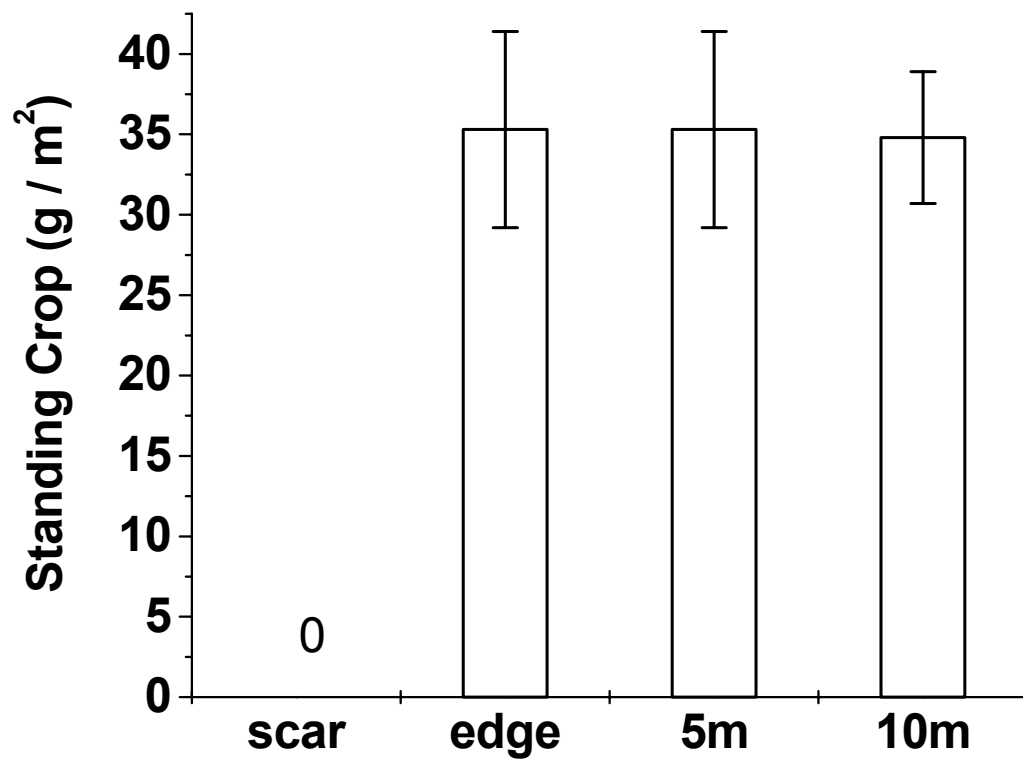


Figure 8. Mean (S. E.) standing crop (g per m²) across all vegetated treatments (N = 10).

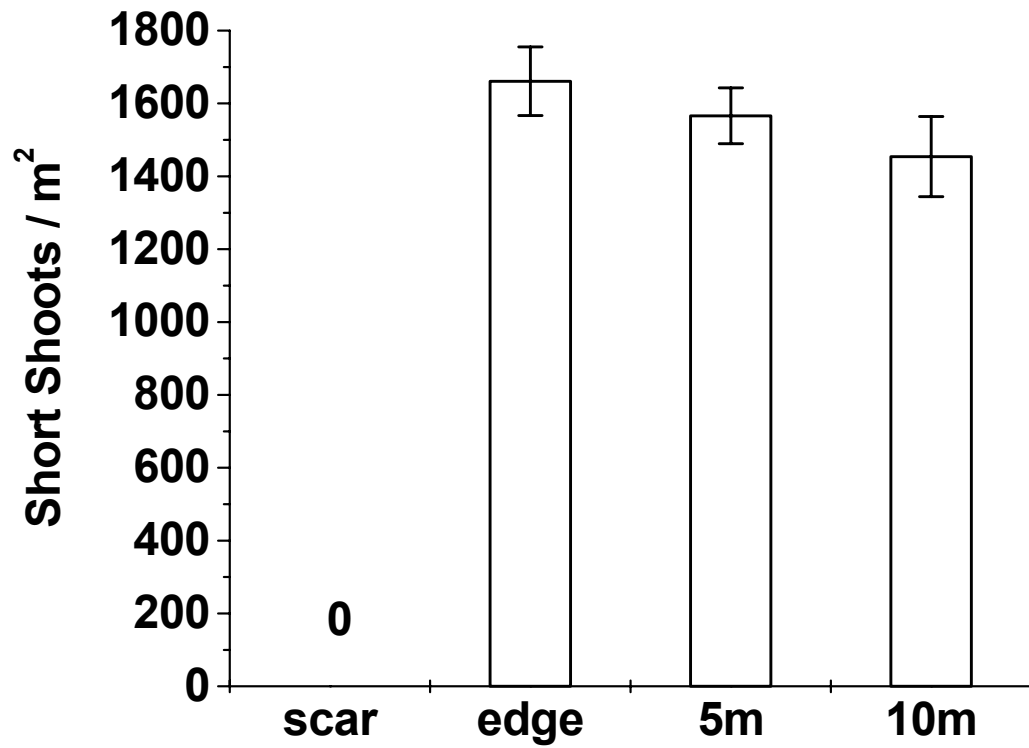


Figure 9. Mean (S. E.) short shoot density (shoots per m²) across all vegetated treatments (N = 10).

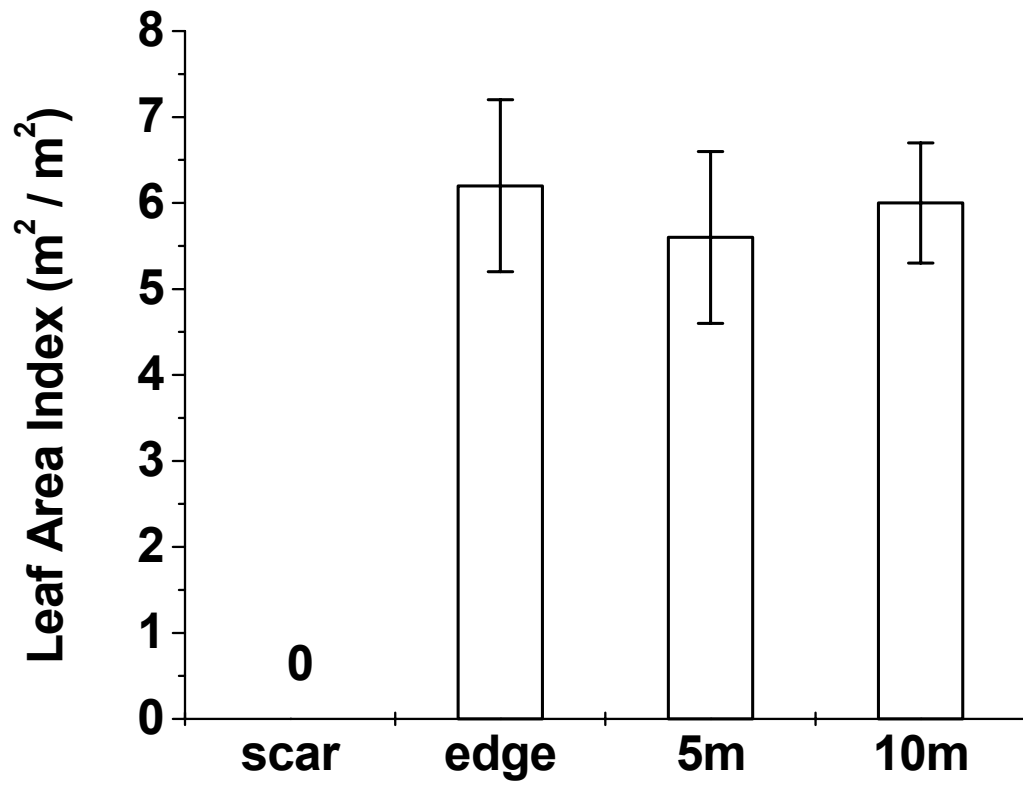


Figure 10. Mean (S. E.) leaf area index (m² per m²) across all vegetated treatments (N = 10).

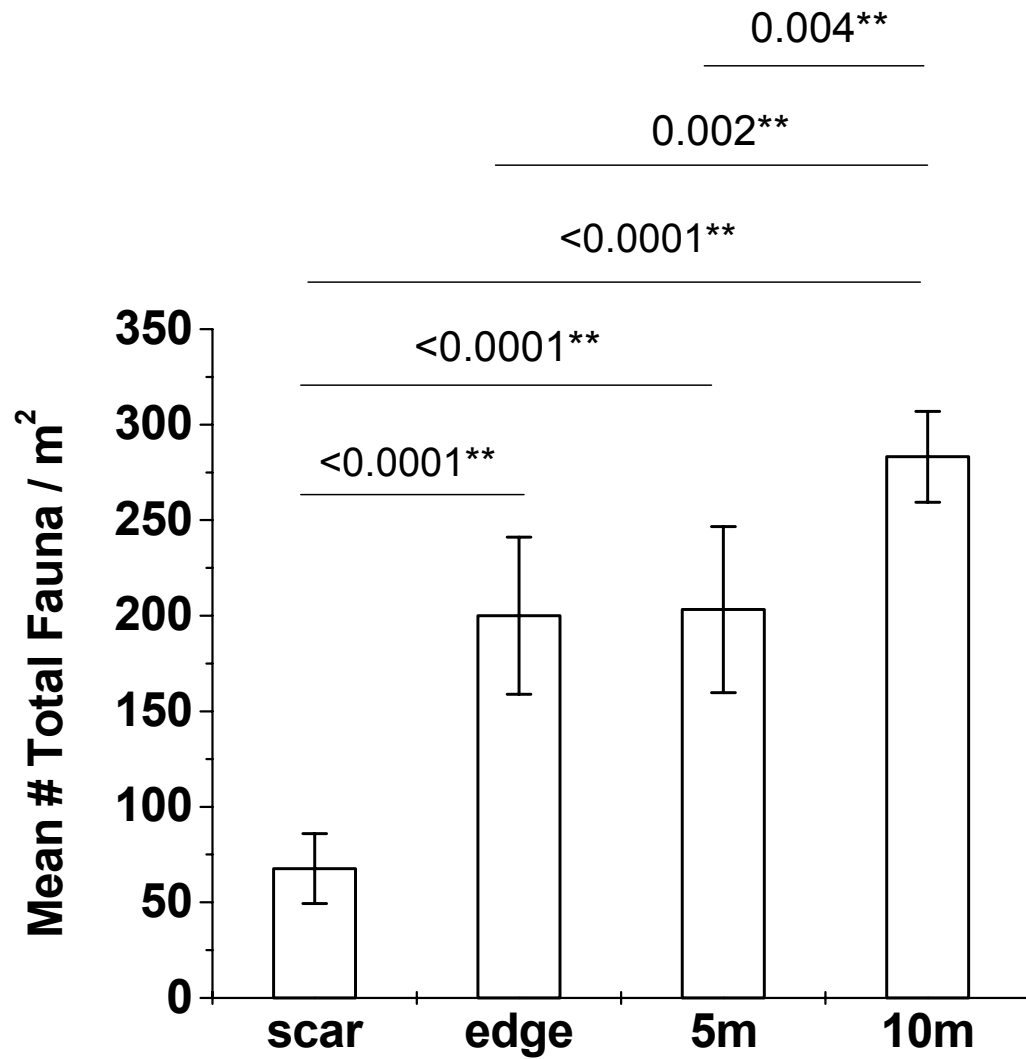


Figure 11. Mean (S. E.) total fauna abundance (# per m²) across all treatments (N = 10). **significant after correcting for multiple comparisons

3.d Fauna

Propeller scars supported significantly fewer numbers of total animals when compared with the surrounding seagrass (Table 2 and 3, Figure 11). In addition, the edge and 5 m treatments contained significantly fewer animals than the 10 m treatment (Table 3, Figure 11). Significantly fewer species were found in scars versus the other treatments (Table 3, Figure 12). Species numbers did not differ significantly between the edge, 5 m, and 10 m treatments (Table 3, Figure 12). There was no significant interaction between treatment and the 13 most abundant taxa (Table 4, Figures 13, 14, 15, and 16).

3.d.1. Shrimps

A total of fourteen species of shrimps (Decapoda) were collected (Table 5). The total number of shrimps per m² was significantly lower in the scar habitat type when compared to the edge, 5 m, and 10 m treatments (Tables 6 and 7, Figure 17). No other treatment comparisons were significantly different (Table 7).

Five species accounted for 93.0 % of the total number of shrimps: *Thor manningi* (24.5 %), *Hippolyte zostericola* / *pleuracanthus* (22.9 %), *Alpheus normanni* (19.5 %), *Periclimenes americanus* (13.4 %), and *Latreutes fucorum* (12.7 %; Table 5). The most abundant shrimp species was *T. manningi* with a total average density of 71.4 individuals per m² across all treatments (Table 6). *T. manningi* had significantly higher densities in the edge, 5 m, and 10 m treatments versus the scar (Table 7, Figure 18).

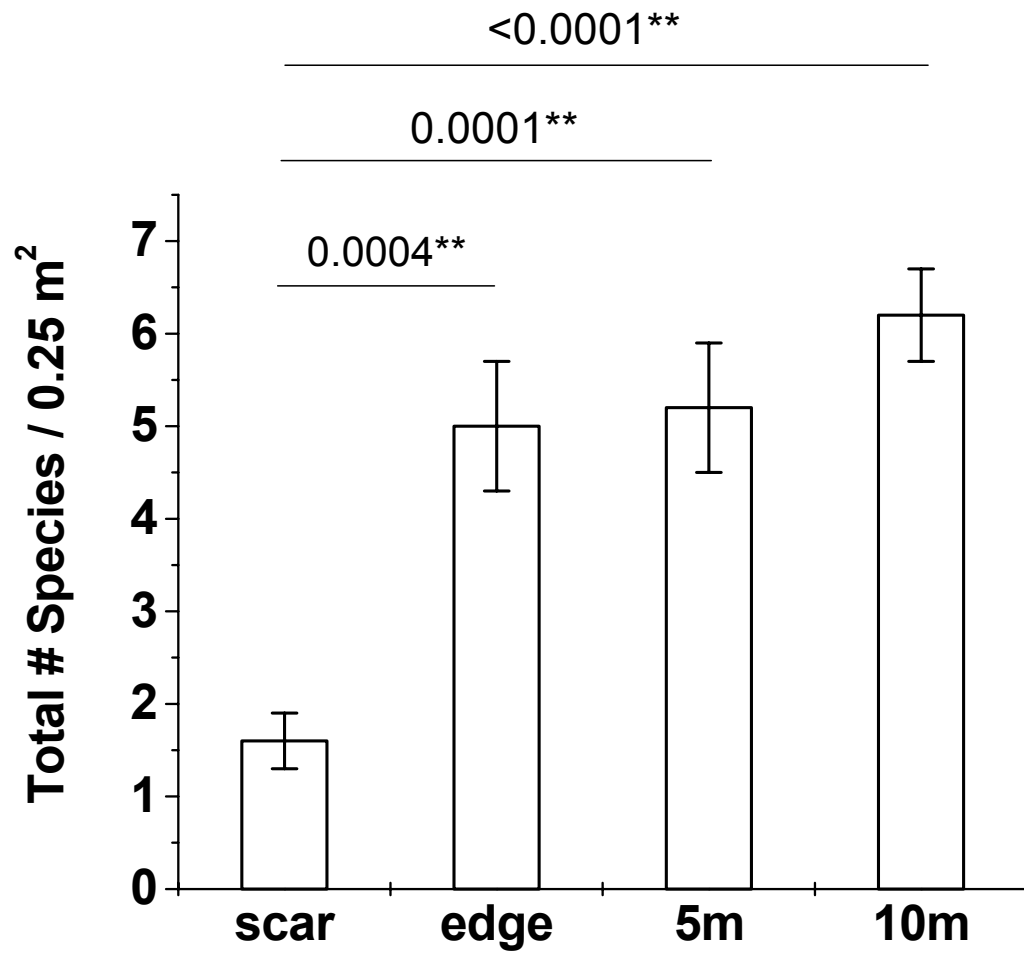


Figure 12. Mean (S. E.) number of species (# per 0.25 m²) across all treatments (N = 10). **significant after correcting for multiple comparisons

Table 4. Results of the two-way ANOVA testing for the interaction of treatment and taxa. * indicates significance

Source	df	SS	MS	F value	P value
block	9	13.60	1.51	5.71	<0.0001*
treatment	3	21.56	7.19	27.17	<0.0001*
taxa	12	55.09	4.59	17.35	<0.0001*
treatment x taxa	36	13.10	0.36	1.38	0.0764
error	459	121.4	0.26		
total	519	224.8			

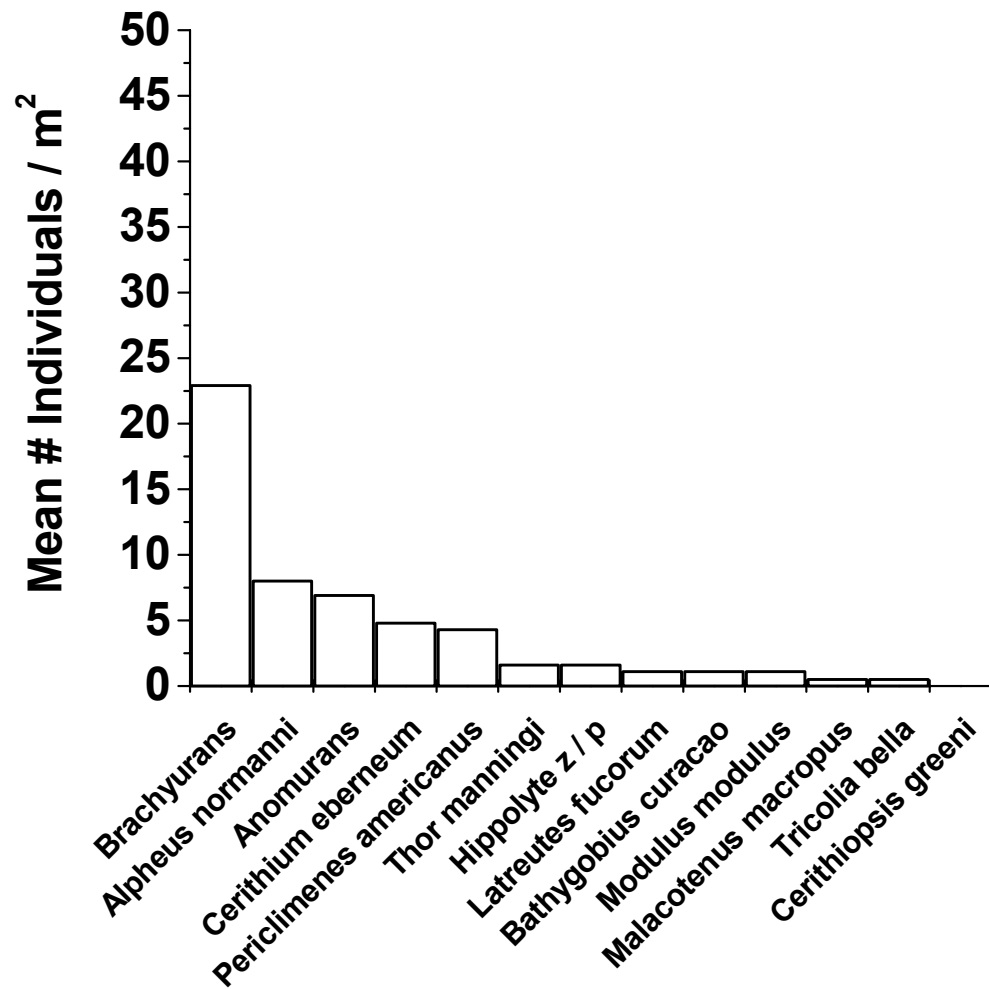


Figure 13. Rank abundance for all animals in scars. *Hippolyte zostericola* / *pleuracanthus* is abbreviated as “*Hippolyte z / p*”.

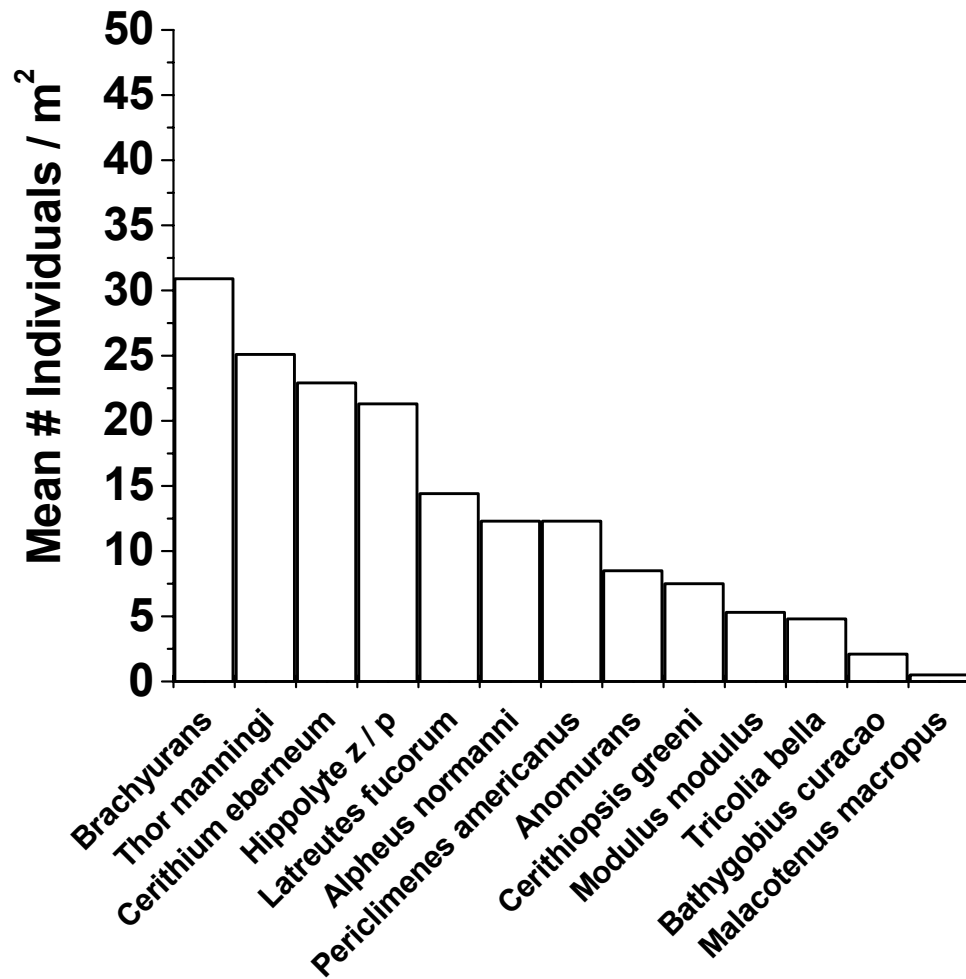


Figure 14. Rank abundance for all animals in edges. *Hippolyte zostericola* / *pleuracanthus* is abbreviated as “*Hippolyte z / p*”.

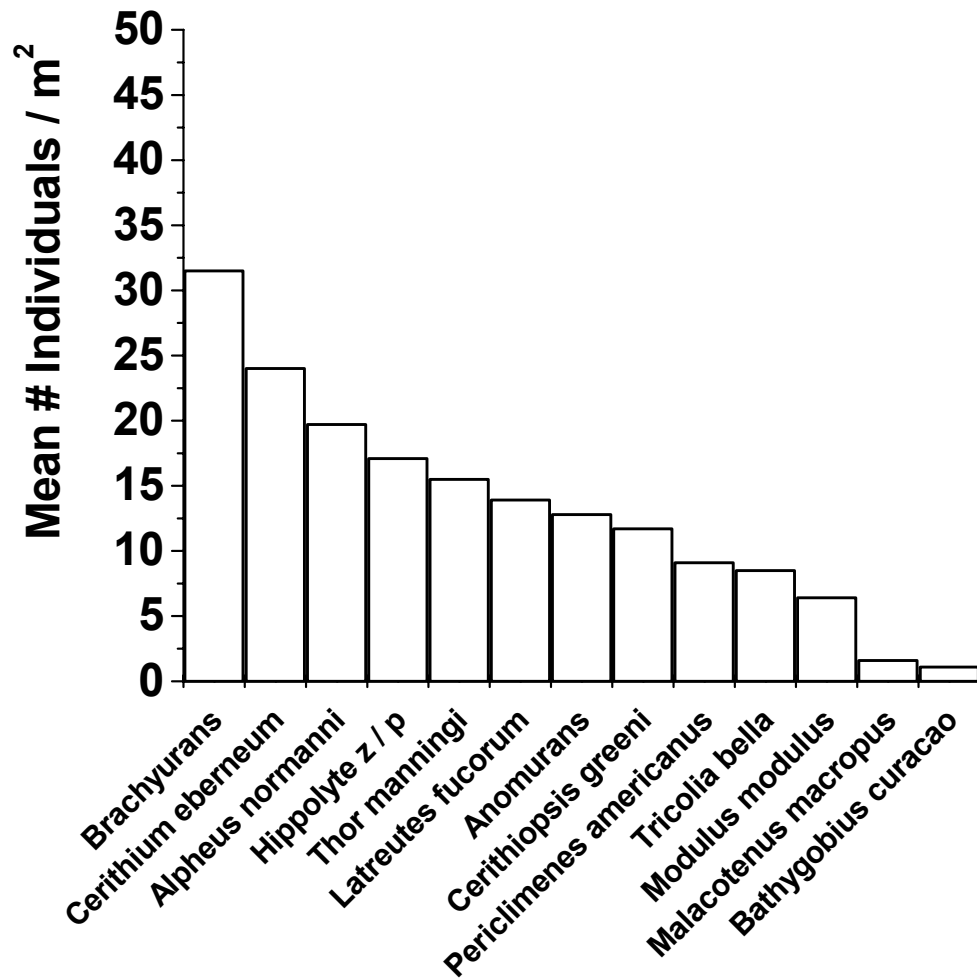


Figure 15. Rank abundance for all animals in the 5 m treatments.
Hippolyte zostericola / pleuracanthus is abbreviated as “*Hippolyte z / p*”.

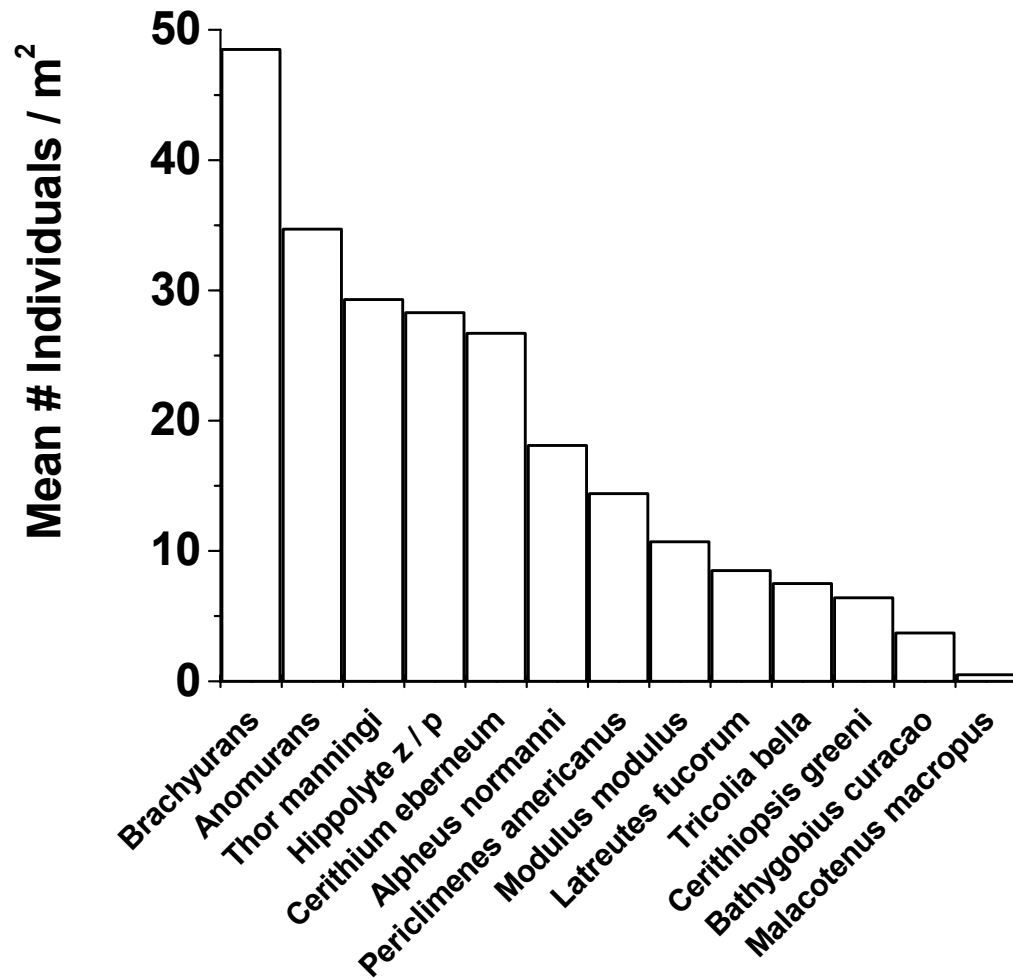


Figure 16. Rank abundance for all animals in the 10 m treatments.
Hippolyte zostericola / *pleuracanthus* is abbreviated as “*Hippolyte z / p*”.

Table 5. Number and percent composition of shrimps collected across all treatments.

Shrimp Taxon	# Individuals	Percent
<i>Thor manningi</i>	137	24.5
<i>Hippolyte zostericola</i> / <i>pleuracanthus</i> [†]	128	22.9
<i>Alpheus normanni</i>	109	19.5
<i>Periclimenes americanus</i>	75	13.4
<i>Latreutes fucorum</i>	71	12.7
<i>Trachypenaeus</i> sp.	14	2.5
<i>Processa bermudensis</i>	12	2.1
<i>Leander tenuicornis</i>	6	1.1
<i>Latreutes parvulus</i>	2	0.4
<i>Tozeuma carolinense</i>	2	0.4
<i>Sicyonia laevigata</i>	1	0.2
<i>Farfantepenaeus duorarum</i>	1	0.2
<i>Metapenaeopsis goodei</i>	1	0.2
Total Shrimps	559	

[†]treated as a complex of the two species (Gore et al., 1981)

Table 6. Mean (S. E.) number of shrimps per m² within each treatment (N = 10).

Shrimp Taxon	scar	edge	5 m	10 m
<i>Thor manningi</i>	1.6 (1.6)	25.0 (6.5)	15.5 (5.1)	29.3 (10.1)
<i>Hippolyte zostericola</i> / <i>pleuracanthus</i> [†]	1.6 (1.1)	21.3 (10.5)	17.1 (6.0)	28.3 (21.9)
<i>Alpheus normanni</i>	8.0 (3.0)	12.3 (5.4)	19.7 (4.1)	18.1 (7.0)
<i>Periclimenes americanus</i>	4.3 (2.1)	12.3 (5.2)	9.1 (2.6)	14.4 (6.3)
<i>Latreutes fucorum</i>	1.1 (0.7)	14.4 (4.6)	13.9 (4.3)	8.5 (4.2)
Pooled Shrimps ^{††}	6.9 (3.0)	4.3 (1.7)	2.7 (1.2)	6.9 (1.1)
Total Shrimps	23.5 (4.5)	89.6 (21.2)	78.0 (14.7)	105.5 (20.0)

[†]treated as a complex of the two species (Gore et al., 1981)

^{††}includes: *Trachypenaeus* sp.
Processa bermudensis
Metapenaeopsis goodei
Farfantepenaeus duorarum
Sicyonia laevigata
Leander paulensis
Tozeuma carolinense
Latreutes parvulus
Leander tenuicornis

Table 7. P-values resulting from paired, two-tailed t-tests comparing differences in mean number of shrimps per m² between pairs of treatments. *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons

Shrimp Taxon	scar-- edge	scar-- 5 m	scar-- 10 m	edge-- 5 m	edge-- 10 m	5 m-- 10 m
<i>Thor manningi</i>	0.001**	0.027*	<0.0001**	0.104	0.850	0.141
<i>Hippolyte zostericola / pleuracanthus</i> [†]	0.006**	0.008**	0.0004**	0.616	0.197	0.154
<i>Alpheus normanni</i>	0.564	0.023*	0.252	0.238	0.066	0.824
<i>Periclimenes americanus</i>	0.173	0.151	0.116	0.901	0.616	0.454
<i>Latreutes fucorum</i>	0.029*	0.013*	0.075	0.746	0.570	0.431
Pooled Shrimps ^{††}	0.213	0.122	0.399	0.434	0.030*	0.005**
Total Shrimps	0.006**	0.002**	0.002**	0.506	0.236	0.126

[†]treated as a complex of the two species (Gore et al., 1981)

^{††}includes: *Trachypenaeus sp.*
Processa bermudensis
Metapenaeopsis goodei
Farfantepenaeus duorarum
Sicyonia laevigata
Leander paulensis
Tozeuma carolinense
Latreutes parvulus
Leander tenuicornis

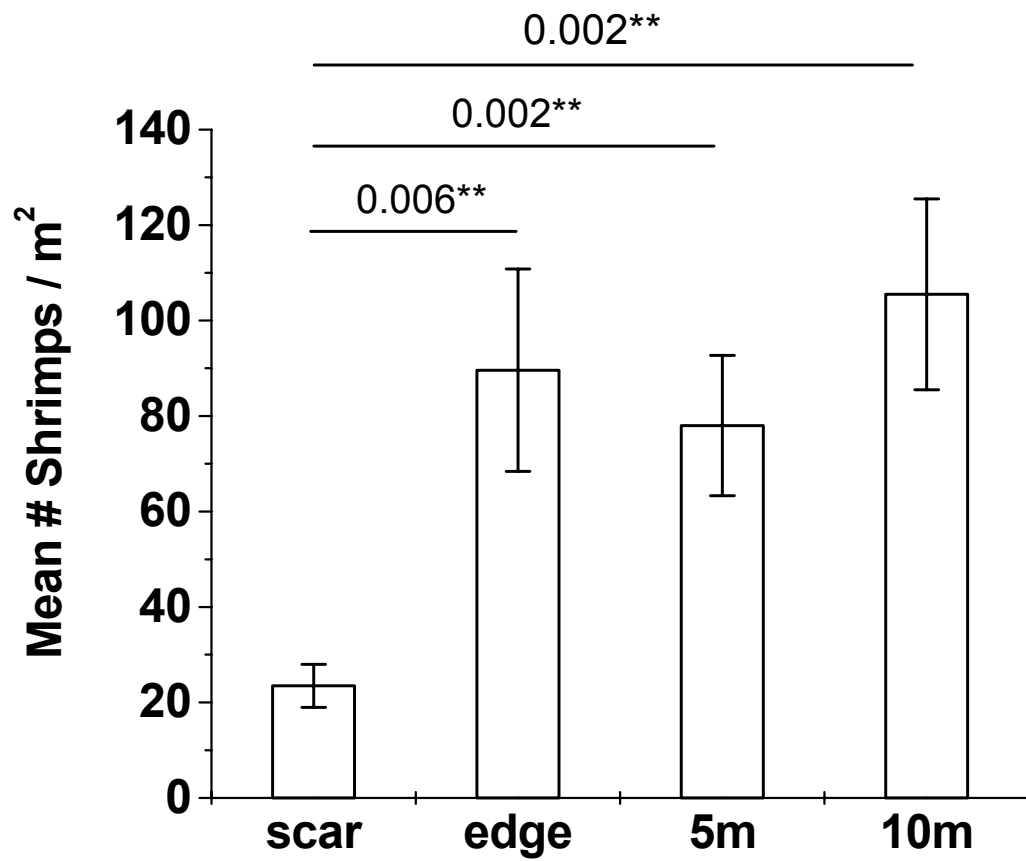


Figure 17. Mean (S. E.) shrimp abundance (# per m²) across all treatments (N = 10). ** significant after correcting for multiple comparisons.

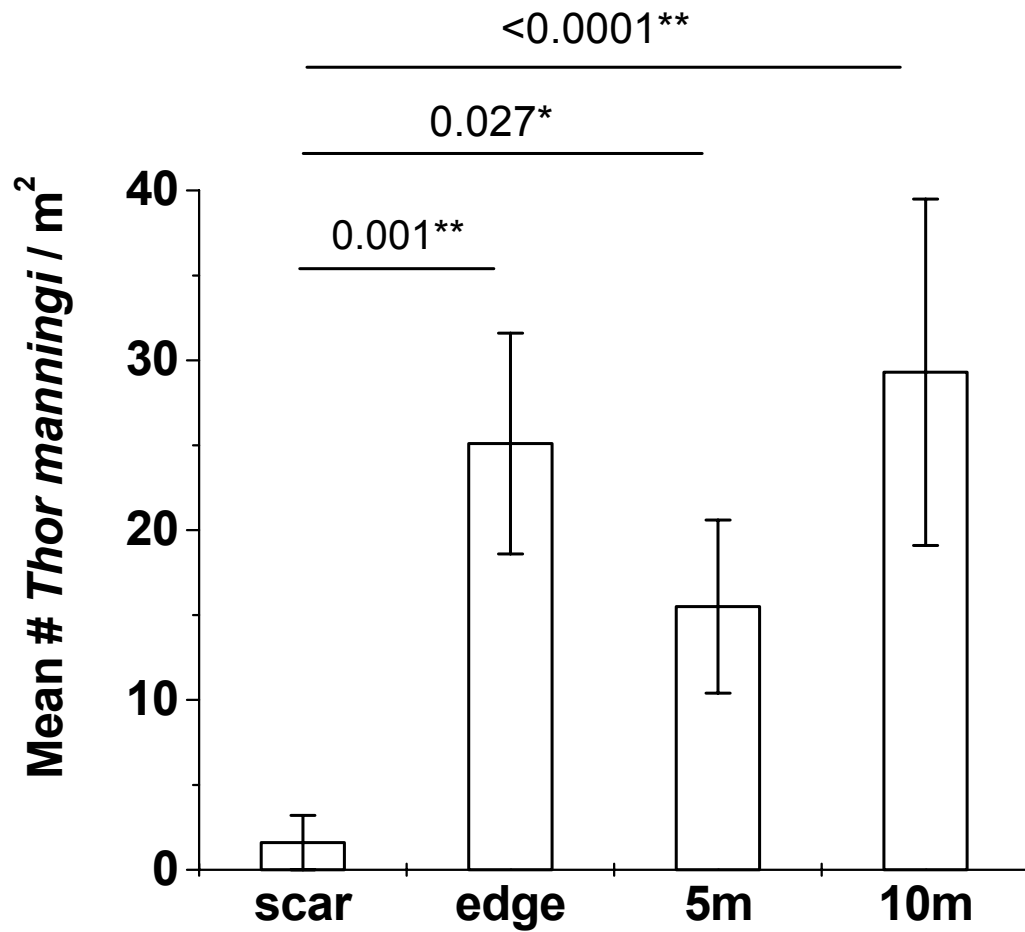


Figure 18. Mean (S. E.) *Thor manningi* abundance (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons

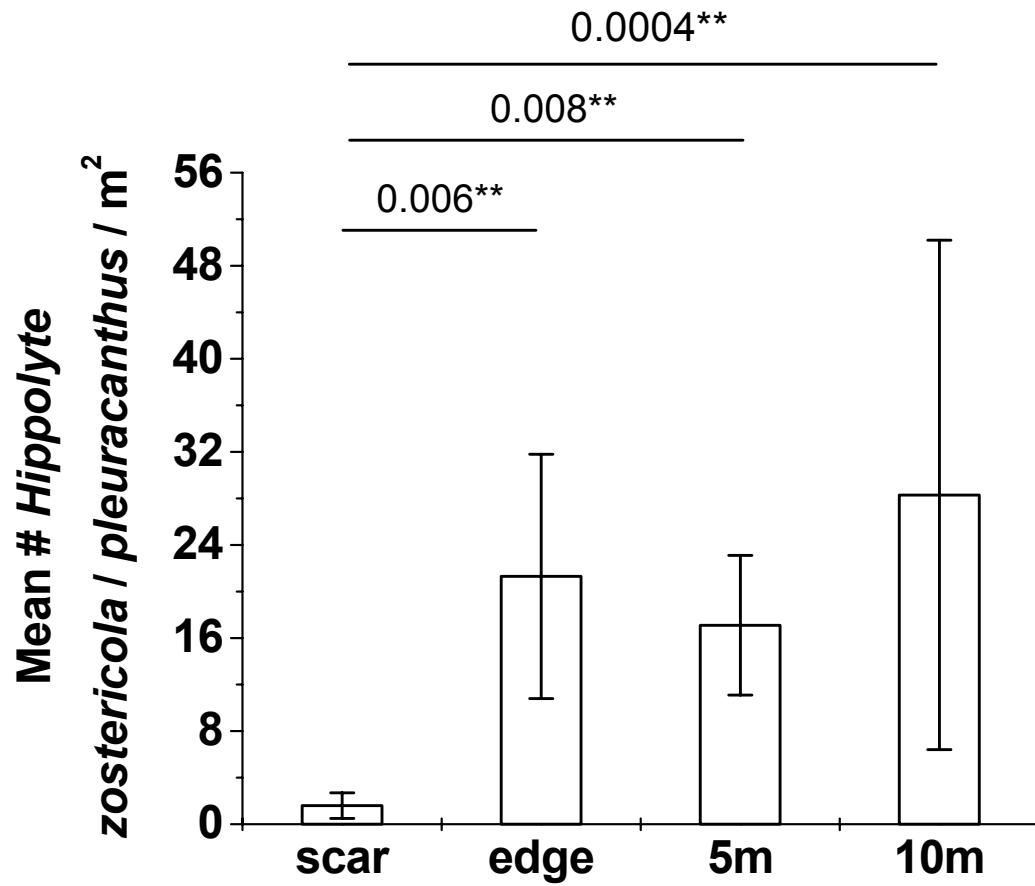


Figure 19. Mean (S. E.) *Hippolyte zostericola / pleuracanthus* abundance (# per m²) across all treatments (N = 10). **significant after correcting for multiple comparisons

Hippolyte zostericola / *pleuracanthus* was the second most abundant shrimp species with a total average density of 68.3 individuals per m² across all treatments (Table 6). These densities were significantly lower in the scar versus the other three treatments (Table 7, Figure 19).

Individuals of the species *Alpheus normanni* accounted for 19.5 % of the total number of shrimps (Table 5). Mean densities of *A. normanni* ranged from 8.0 shrimps per m² in the scar to 19.1 shrimps per m² in the 5 m treatment (Table 6). Densities of this shrimp species were not significantly lower in the scar when compared to the edge and 10 m treatments, but were significantly different between the scar and 5 m treatments (Table 7, Figure 20).

Periclimenes americanus was the fourth most abundant shrimp species with a total mean density of 40.1 individuals per m² across all treatments (Table 6). There were no significant differences in *P. americanus* densities among any of the treatments (Table 7, Figure 21).

Latreutes fucorum accounted for 12.7 % of the total number of shrimps (Table 5). There were significantly lower numbers of *L. fucorum* in the scar versus the edge and 5 m treatments, but no significant difference between the scar and 10 m treatments (Table 7, Figure 22). No other contrasts were significantly different for this species.

Because of very low densities, data for the remaining eight shrimp taxa were pooled. Only the edge-10 m and the 5 m-10 m comparisons yielded significant differences (Table 7, Figure 23).

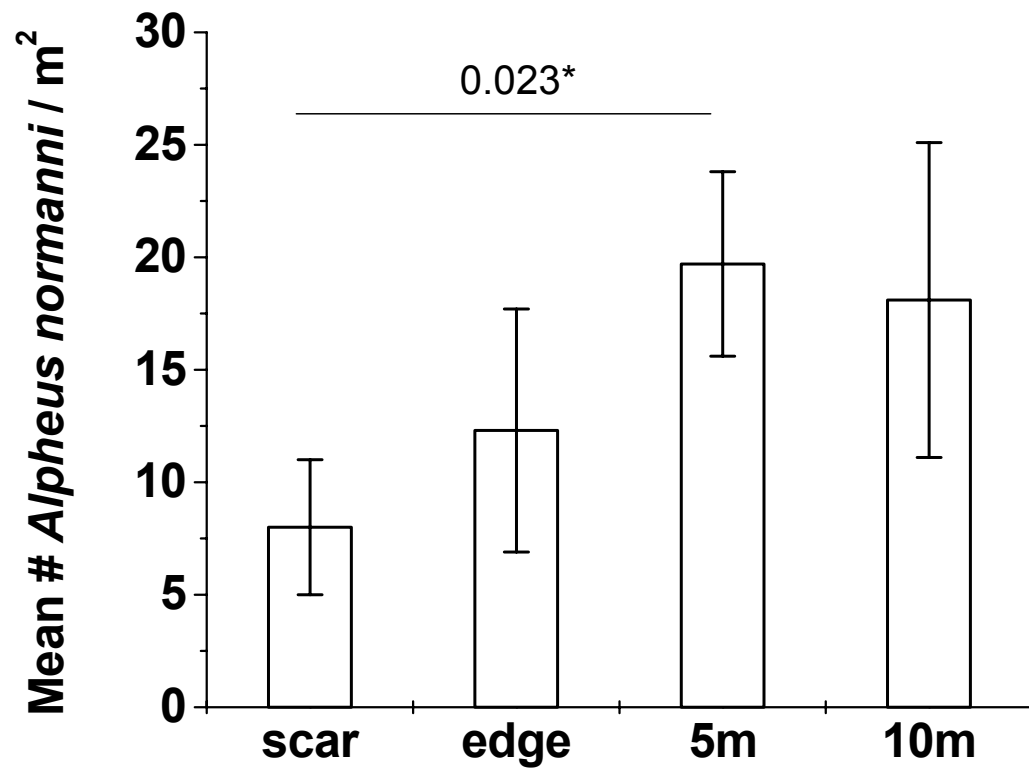


Figure 20. Mean (S. E.) *Alpheus normanni* abundance (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05)

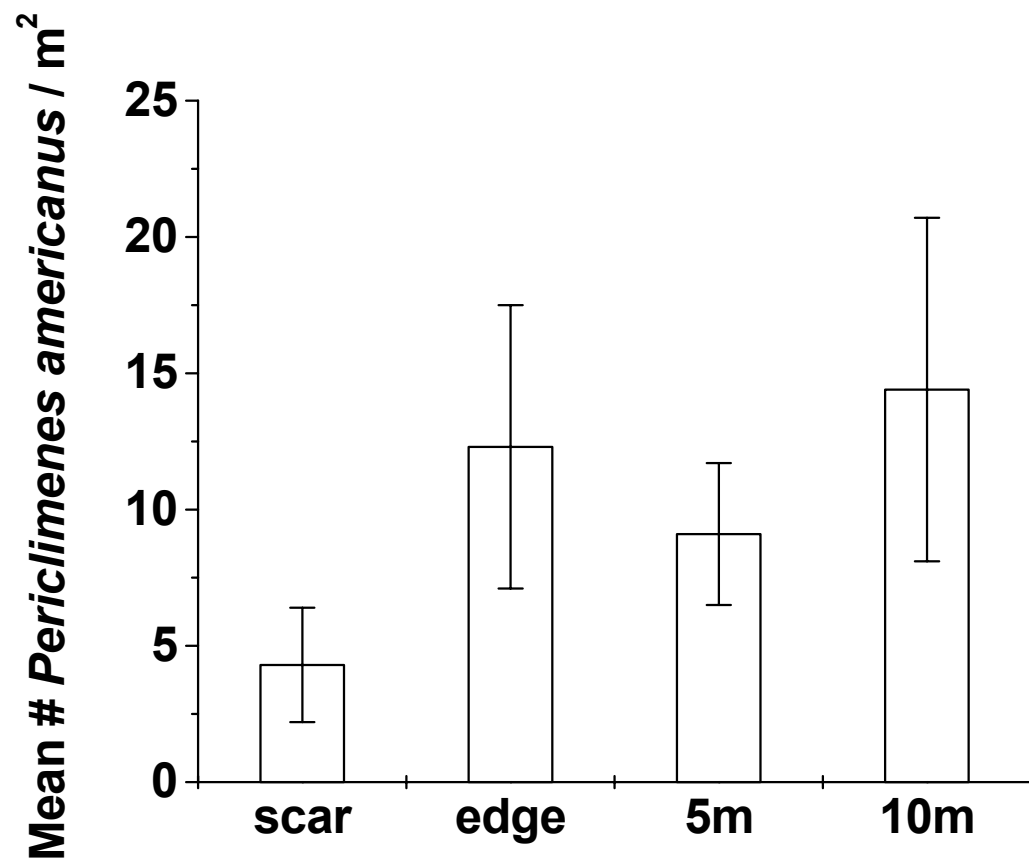


Figure 21. Mean (S. E.) *Periclimenes americanus* abundance (# per m²) across all treatments (N = 10). No contrasts were significant.

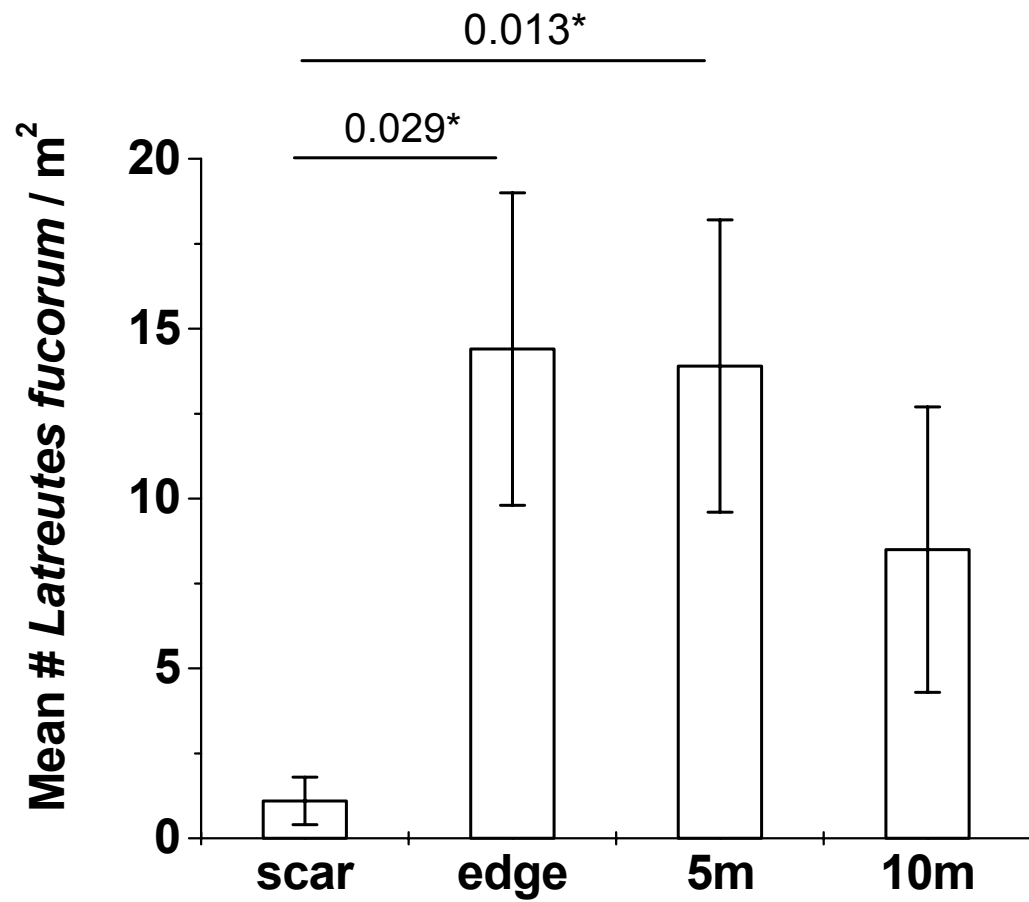


Figure 22. Mean (S. E.) *Latreutes fucorum* abundance (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05)

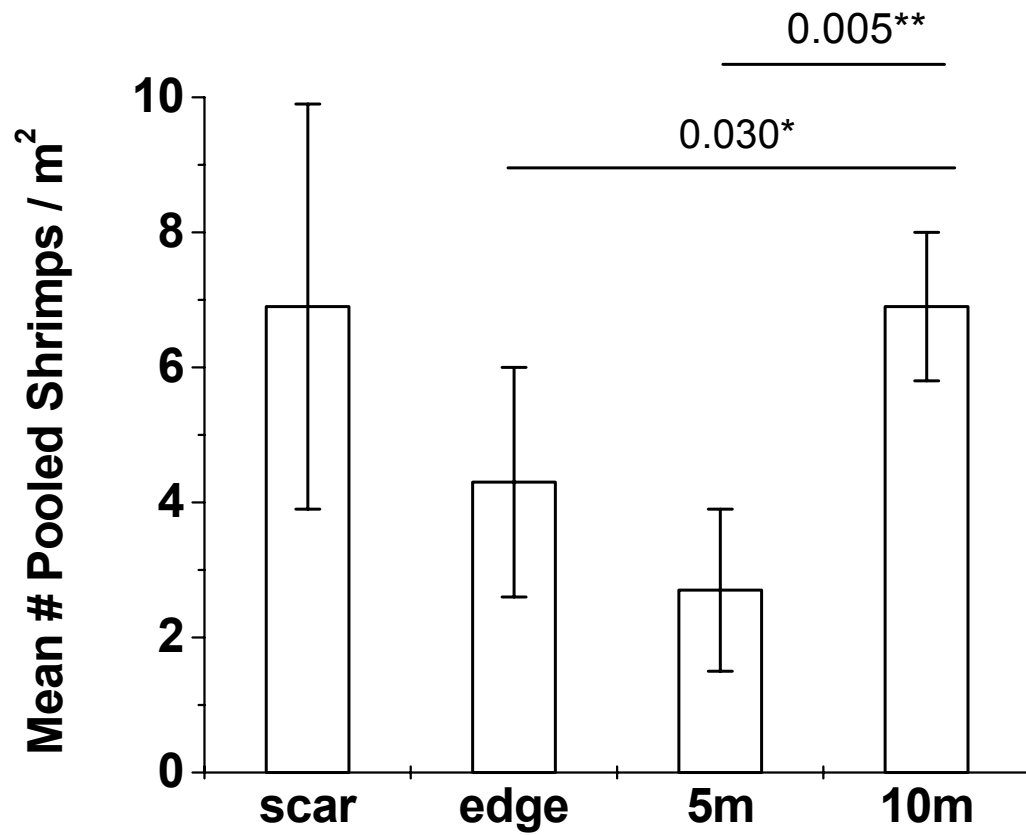


Figure 23. Mean (S. E.) abundance of pooled shrimps (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons

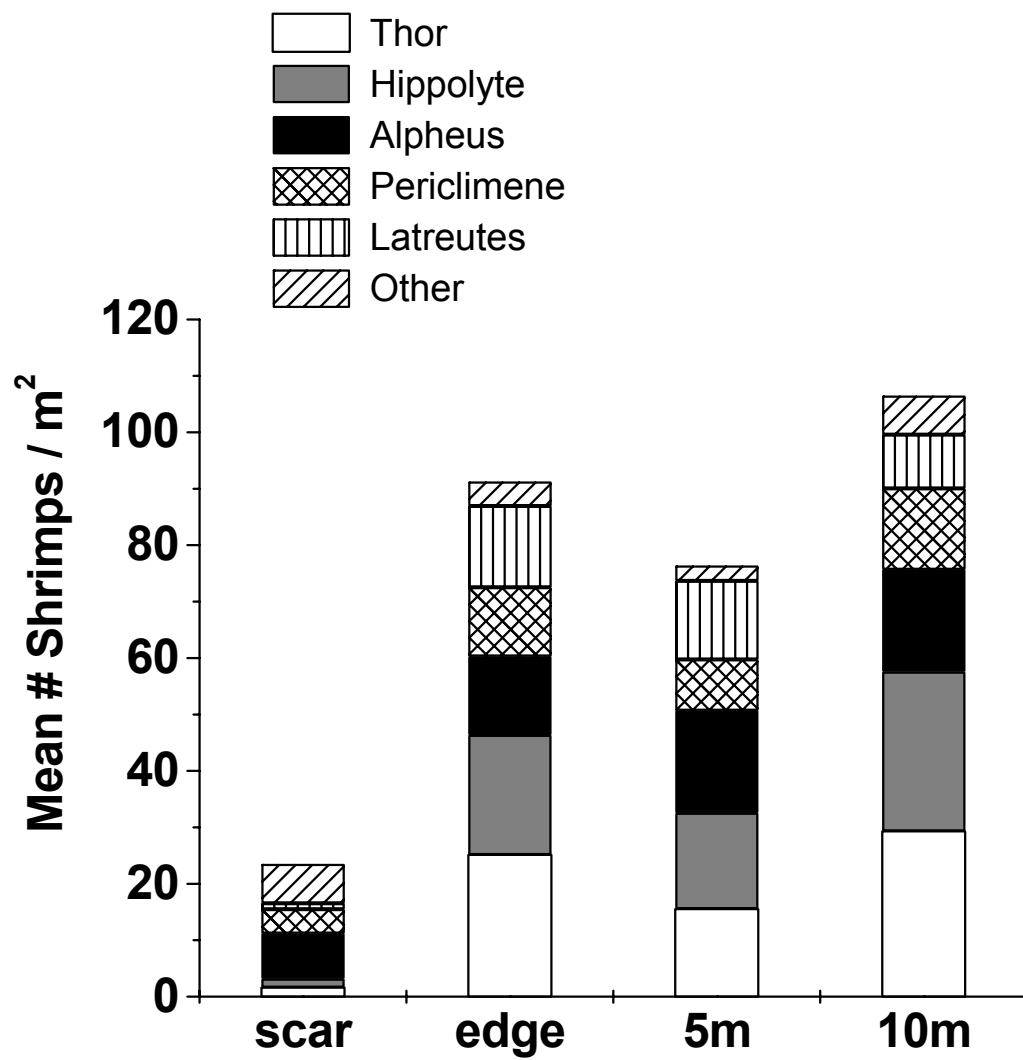


Figure 24. Percent composition of all shrimps across all treatments. Means are presented.

Shrimp assemblages in scars differed from the adjacent seagrass (Figure 24). *Thor manningi* and *Hippolyte zostericola* / *pleuracanthus*, dominant seagrass occupants, were not as proportionally abundant in the scars as in the seagrass habitat types. Individuals of *Alpheus normanni*, *Trachypenaeus* sp., and *Periclimenes americanus* formed the highest proportion of shrimps in propeller scars (Figure 25). Rank abundance plots indicate low evenness across all habitat types although scars were somewhat more even than seagrass habitat (Figures 25, 26, 27, and 28).

3.d.2. Fishes

A total of 26 fishes comprising six species were collected with densities ranging from 2.6 to 5.3 fish per m² (Tables 8 and 9). Two species accounted for 76.9 % of the total fish: *Malacotenus macropus* (53.8 %) and *Bathygobius curacao* (23.1 %; Table 8). For total number of fishes, only the comparison of the edge and 10 m treatments was significantly different (Table 10, Figure 29).

Malacotenus macropus represented 53.8 % of the total fish collected (Table 8). There were no significant differences in *M. macropus* densities among any of the treatments (Table 10, Figure 30).

Bathygobius curacao comprised 23.1 % of the fish collection (Table 8). There were no significant differences in *B. curacao* densities among any of the treatments (Table 10, Figure 31).

None of the pooled fish species were collected from the edge treatments (Table 9). As such, by definition, edge treatments differed significantly from the

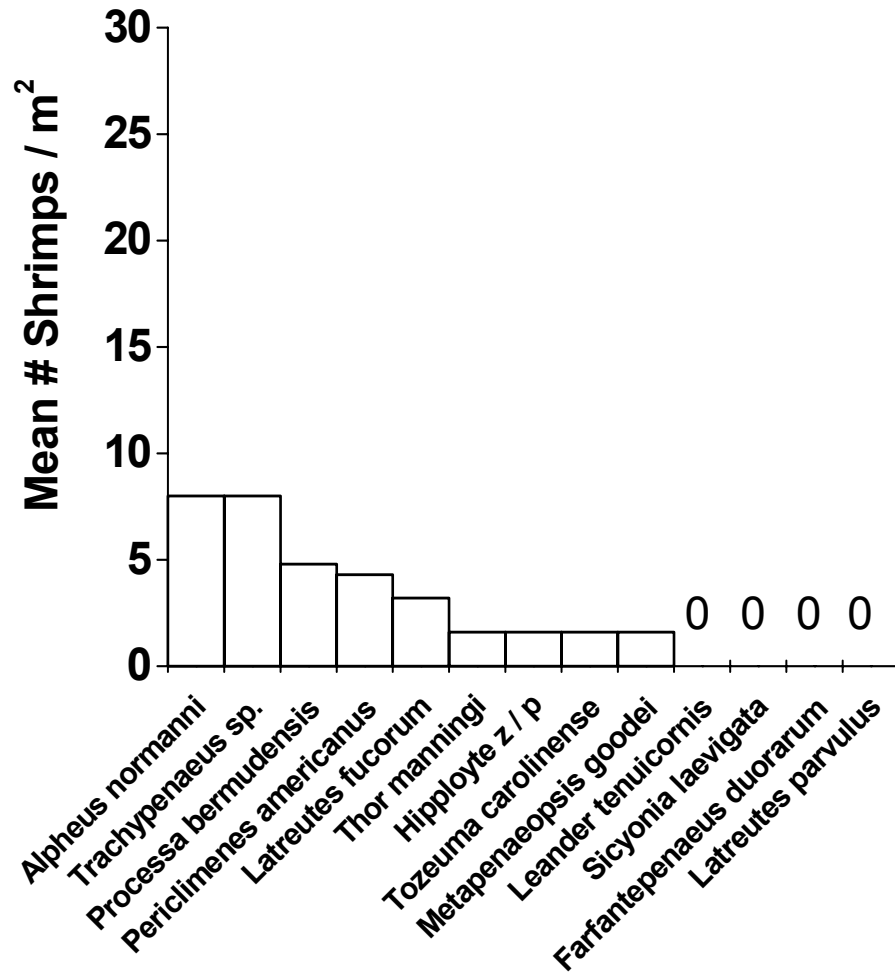


Figure 25. Rank abundance for shrimps in scars. *Hippolyte zostericola* / *pleuracanthus* is abbreviated as “*Hippolyte z / p*”.

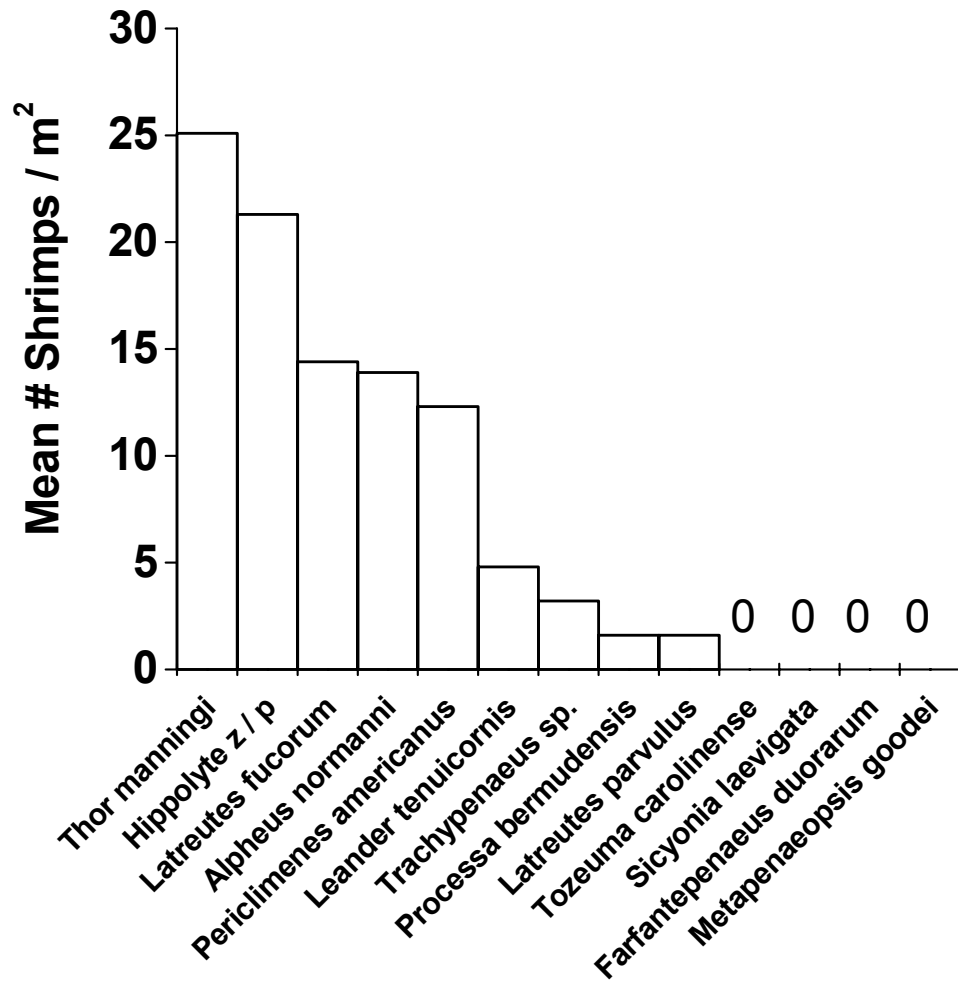


Figure 26. Rank abundance for shrimps in edges. *Hippolyte zostericola* / *pleuracanthus* is abbreviated as “*Hippolyte z / p*”.

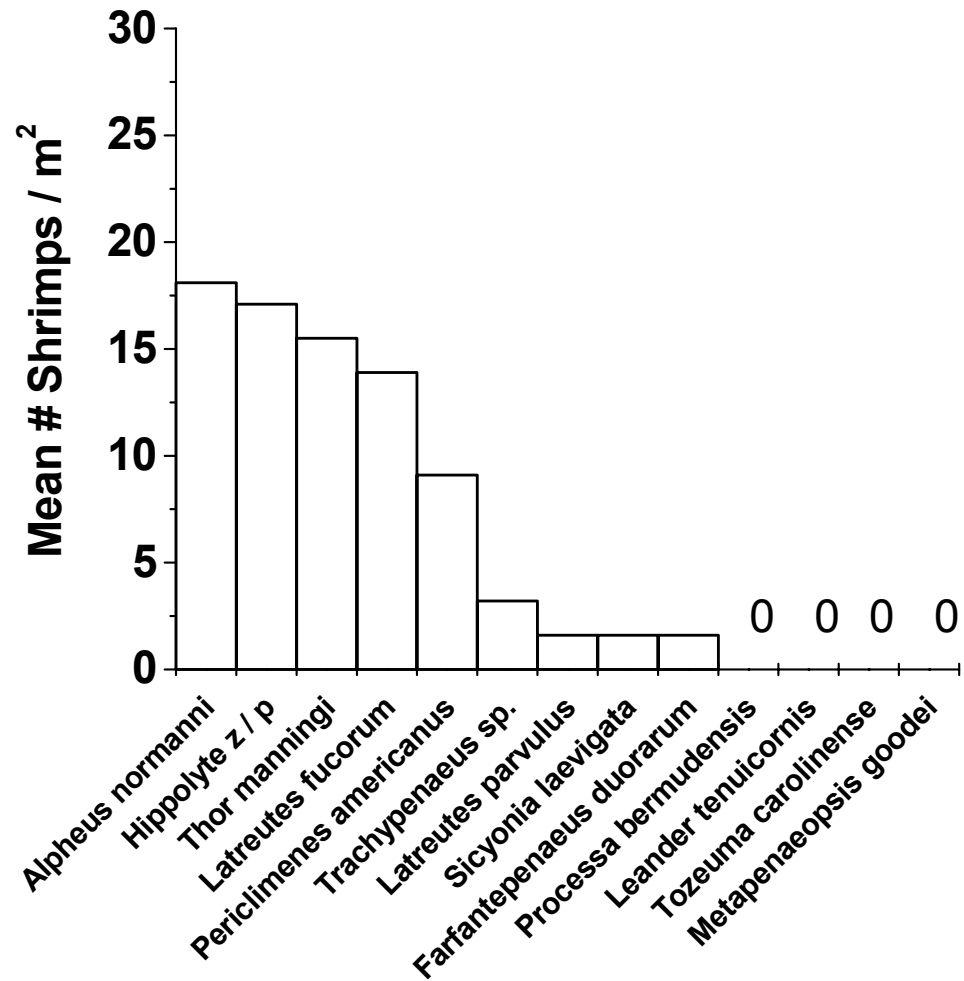


Figure 27. Rank abundance for shrimps in the 5 m treatments.
Hippolyte zostericola / *pleuracanthus* is abbreviated as “*Hippolyte z / p*”.

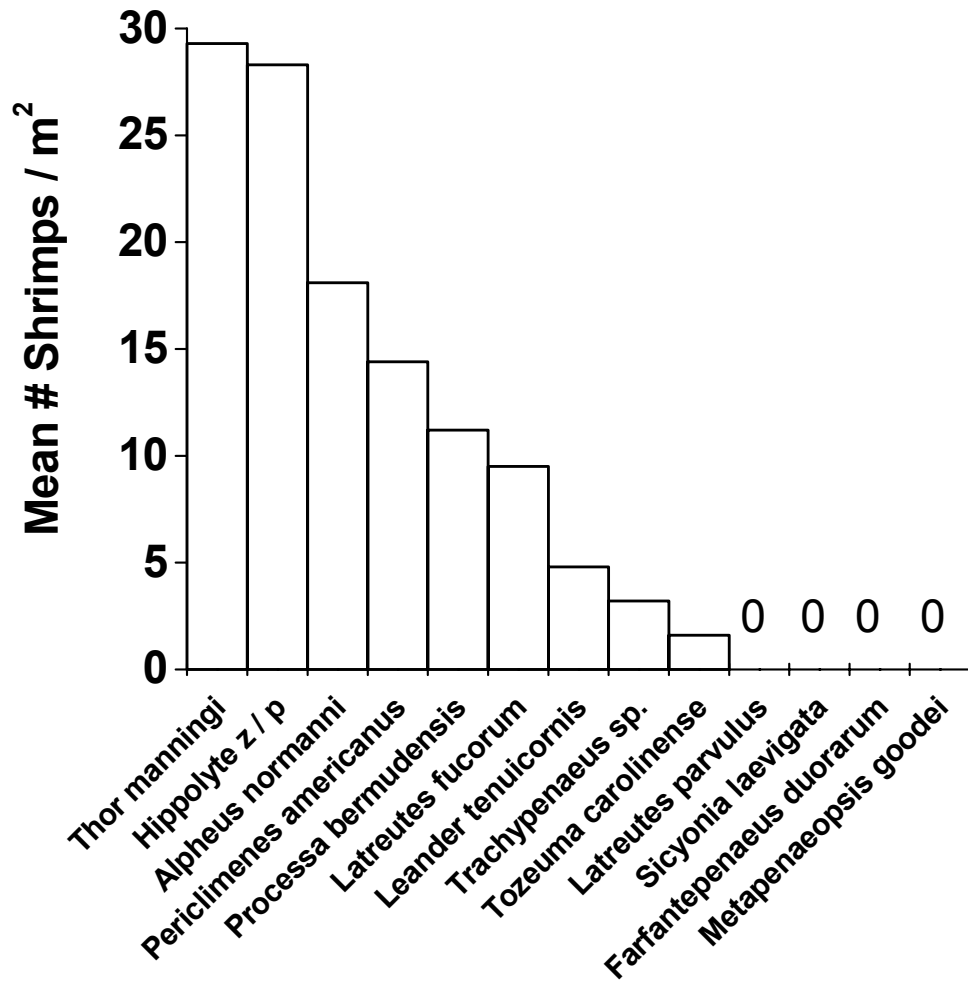


Figure 28. Rank abundance for shrimps in the 10 m treatments. *Hippolyte zostericola* / *pleuracanthus* is abbreviated as “*Hippolyte z / p*”.

Table 8. Number and percent composition of fishes collected across all treatments.

Fish Taxon	# Individuals	Percent
<i>Bathygobius curacao</i>	14	53.8
<i>Malacotenus macropus</i>	6	23.1
<i>Gobionellus saepepallans</i>	2	7.7
<i>F. Gobiidae</i>	1	3.9
<i>Coryphopterus</i> sp.	1	3.9
<i>Bryx dunckeri</i>	1	3.9
<i>Sparisoma</i> sp.	1	3.9
Total Fishes	26	

Table 9. Mean (S. E.) number of fishes per m² within each treatment (N = 10).

Fish Taxon	scar	edge	5 m	10 m
<i>Malacotenus macropus</i>	0.5 (0.5)	0.5 (0.5)	1.6 (1.1)	0.5 (0.5)
<i>Bathygobius curacao</i>	1.1 (0.7)	2.1 (2.1)	1.1 (1.1)	3.7 (2.7)
Pooled Fishes [†]	1.6 (1.1)	0 (0)	0.5 (0.5)	1.1 (0.7)
Total Fishes	3.2 (1.4)	2.6 (2.1)	3.2 (1.4)	5.3 (2.7)

[†]includes: *F. Gobiidae*
Coryphopterus sp.
Bryx dunckeri
Gobionellus saepepallans
Sparisoma sp.

Table 10. P-values resulting from paired, two-tailed t-tests comparing differences in mean number of fishes per m² between pairs of treatments.
 *significant at the per-contrast error rate (alpha = 0.05); N/A = insufficient data to run analysis

Fish Taxon	scar-- edge	scar-- 5 m	scar-- 10 m	edge-- 5 m	edge-- 10 m	5 m-- 10 m
<i>Malacotenus macropus</i>	1.000	0.500	1.000	0.750	1.000	0.750
<i>Bathygobius curacao</i>	1.000	1.000	0.500	1.000	0.500	0.500
Pooled Fishes [†]	N/A	0.675	0.139	N/A	N/A	0.140
Total Fishes	0.722	1.000	0.434	0.777	0.037*	0.541

[†]includes: *F. Gobiidae*
Coryphopterus sp.
Bryx dunckeri
Gobionellus saepepallans
Sparisoma sp.

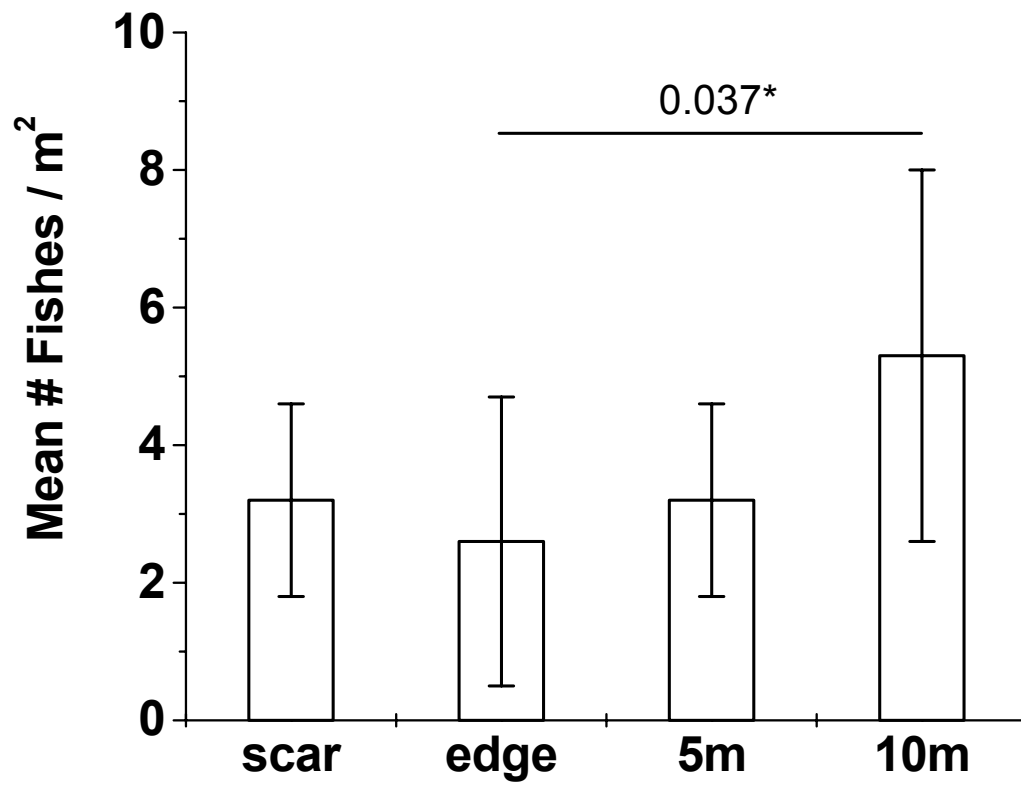


Figure 29. Mean (S. E.) abundance of fishes (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05)

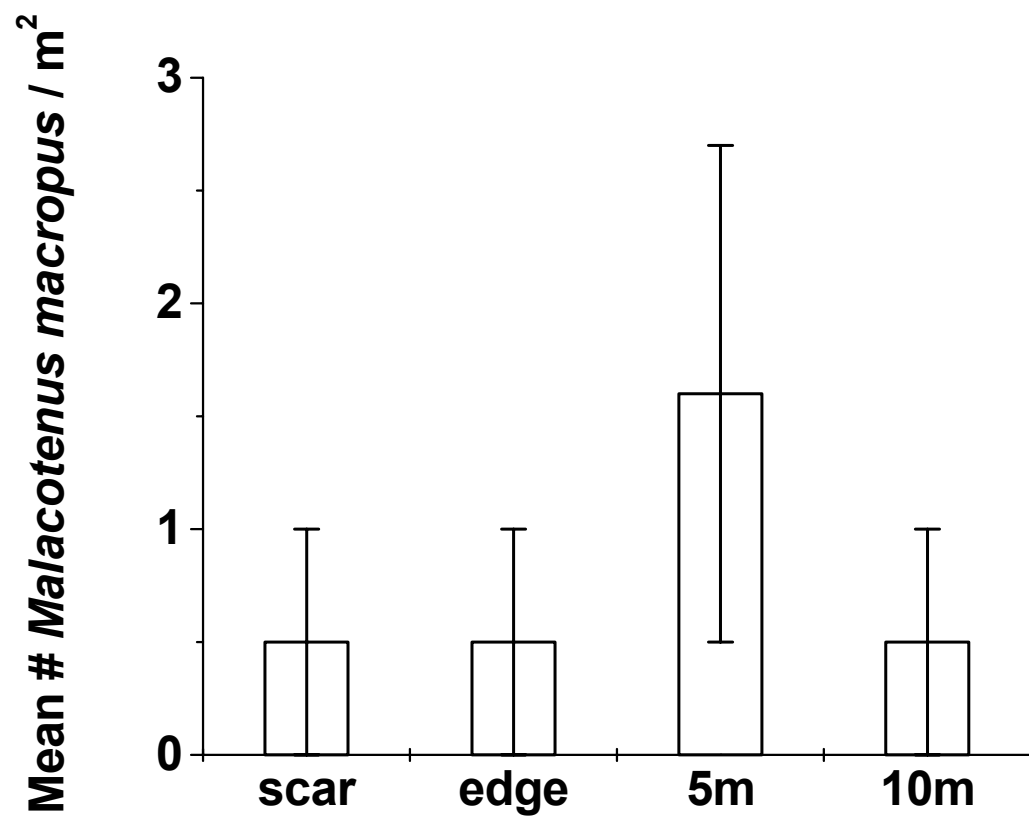


Figure 30. Mean (S. E.) *Malacotenus macropus* abundance (# per m²) across all treatments (N = 10). No contrasts were significant.

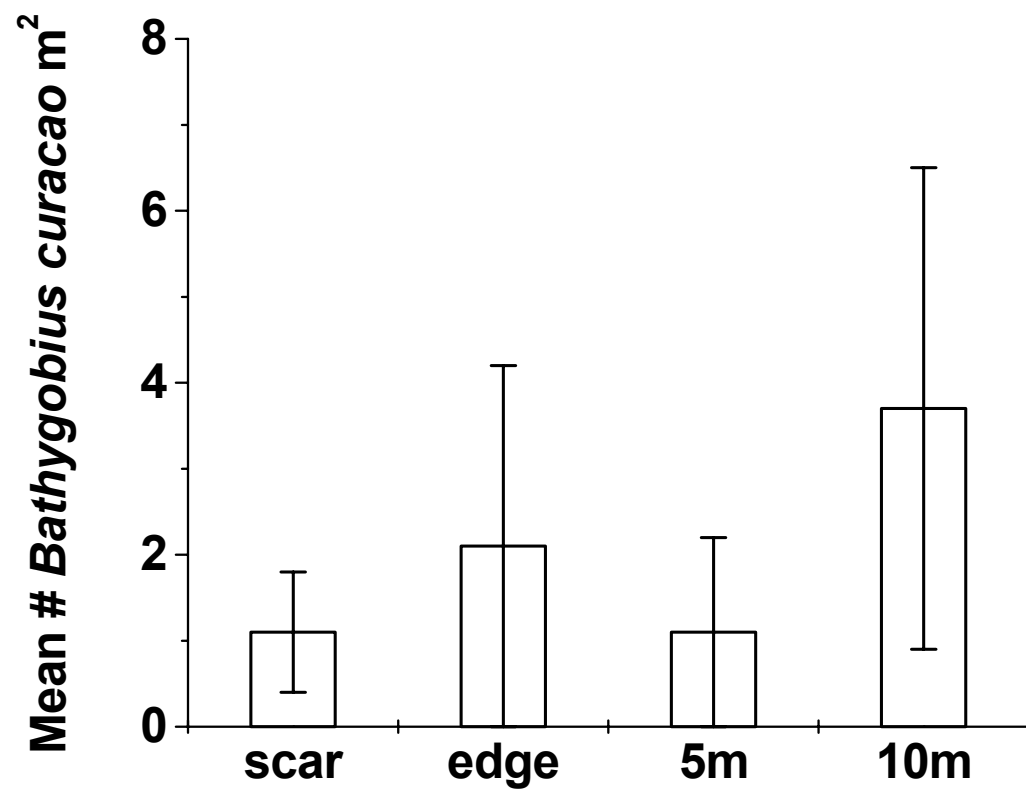


Figure 31. Mean (S. E.) *Bathygobius curacao* abundance (# per m²) across all treatments (N = 10). No contrasts were significant.

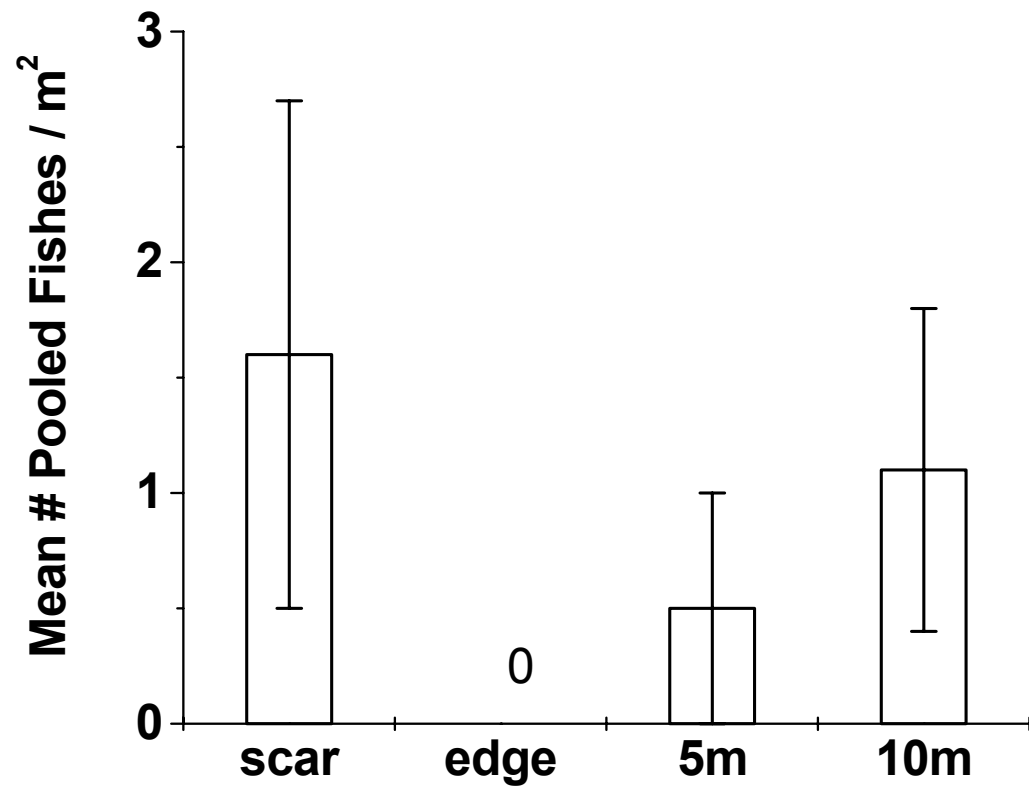


Figure 32. Mean (S. E.) abundance (# per m²) of pooled fishes across all treatments (N = 10).

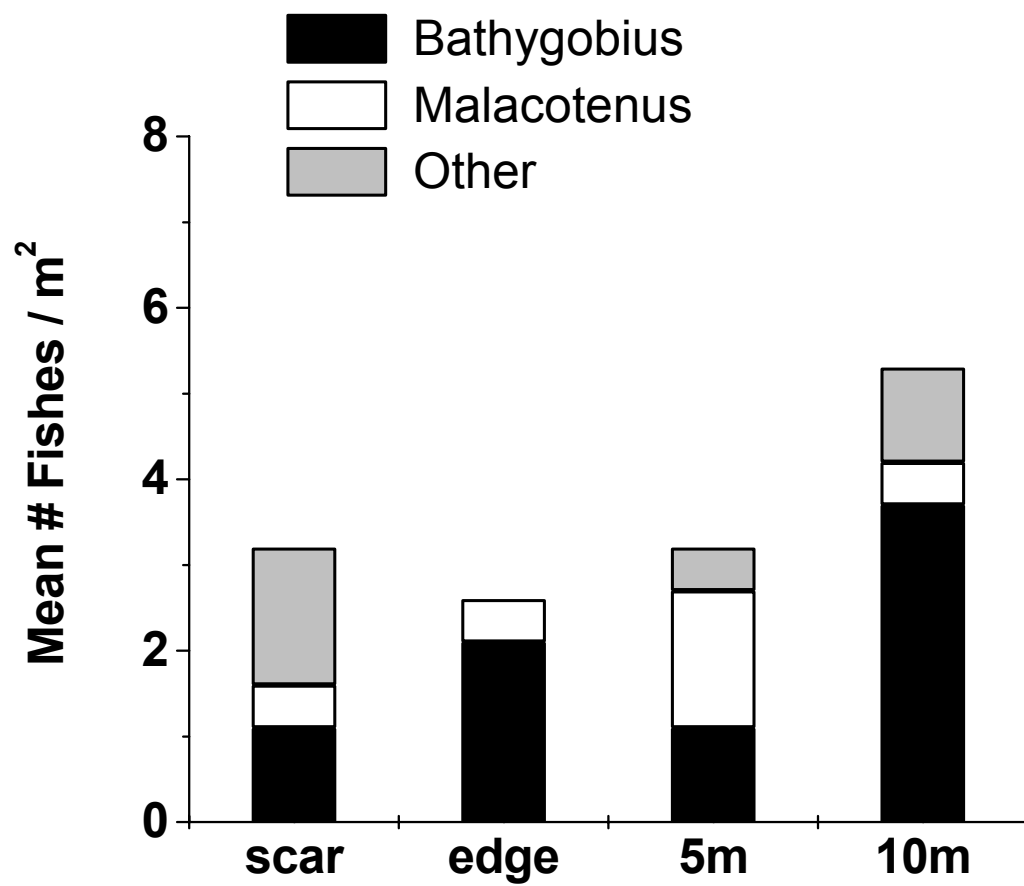


Figure 33. Percent composition of all fishes across all treatments. Means are presented.

remaining treatments. There were no significant differences among the remaining treatments (Table 10, Figure 32). All treatments were dominated by *Bathygobius curacao* and *Malacotenus macropus* (Figure 33).

3.d.3. Crabs

A total of 369 crabs were collected from among all treatments (Table 11). Brachyurans dominated, comprising 68.0 % of the total crabs collected (Table 11). Total crab densities ranged from 29.9 individuals per m² in the scar to 83.2 individuals per m² in the 10 m treatment (Table 12). There were significantly lower numbers of total crabs in the scar, edge and 5 m treatments than in the 10 m treatment (Table 13, Figure 34). Brachyuran densities were significantly lower in the scar and 5 m treatments than in the 10 m treatment (Table 13, Figure 35). Anomuran densities exhibited no significant differences across treatments (Table 13, Figure 36).

3.d.4. Molluscs

A total of 460 molluscs comprised of 30 species were collected (Table 14). The total average density was 245.3 individuals per m² (Table 15). Mollusc density was significantly lower in the scar relative to the other treatments (Table 16, Figure 37). In addition, mollusc densities in the edge and 5 m treatments were significantly lower than in the 10 m treatment (Table 16, Figure 37).

Four species accounted for 60.7 % of total molluscs: *Cerithium eberneum* (32.0 %), *Cerithiopsis greeni* (10.4 %), *Modulus modulus* (9.6 %), and *Tricolia bella* (8.7 %, Table 14). Only the scar-10 m comparison was significantly

Table 11. Number and percent composition of crabs collected across all treatments.

Crab Taxon	# Individuals	Percent
Brachyura	251	68.0
Anomura	118	32.0
Total Crabs	369	

Table 12. Mean (S. E.) number of crabs per m² within each treatment (N = 10).

Crab Taxon	scar	edge	5 m	10 m
Brachyura	22.9 (7.3)	31.0 (9.1)	31.5 (5.1)	48.5 (7.2)
Anomura	7.0 (4.1)	8.5 (9.3)	12.8 (14.2)	34.7 (14.9)
Total Crabs	29.9 (10.8)	39.5 (10.6)	44.3 (7.6)	83.2 (13.7)

Table 13. P-values resulting from paired, two-tailed t-tests comparing differences in mean number of crabs per m² between pairs of treatments. *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons

Crab Taxon	scar-- edge	scar-- 5 m	scar-- 10 m	edge-- 5 m	edge-- 10 m	5 m-- 10 m
Brachyura	0.505	0.359	0.041*	0.952	0.092	0.023*
Anomura	0.364	0.489	0.074	0.971	0.148	0.074
Total Crabs	0.457	0.261	0.020*	0.711	0.031*	0.003**

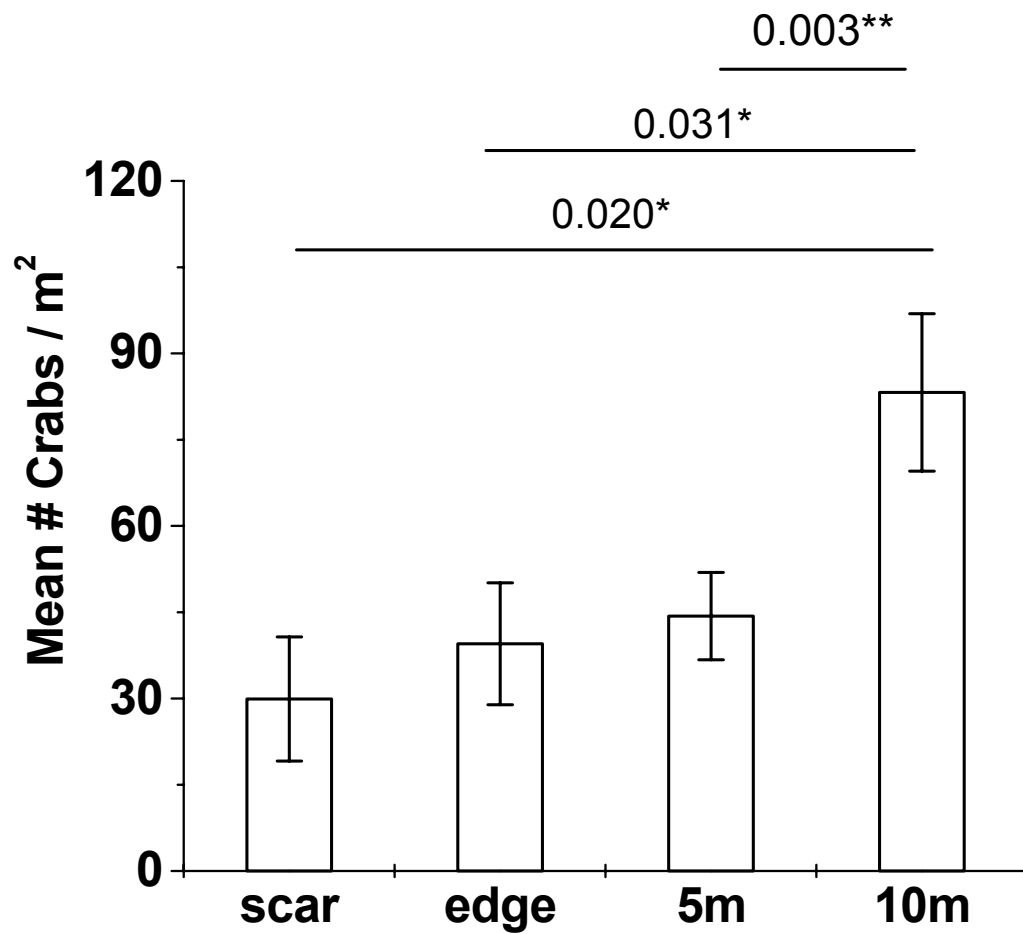


Figure 34. Mean (S. E.) crab abundance (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons

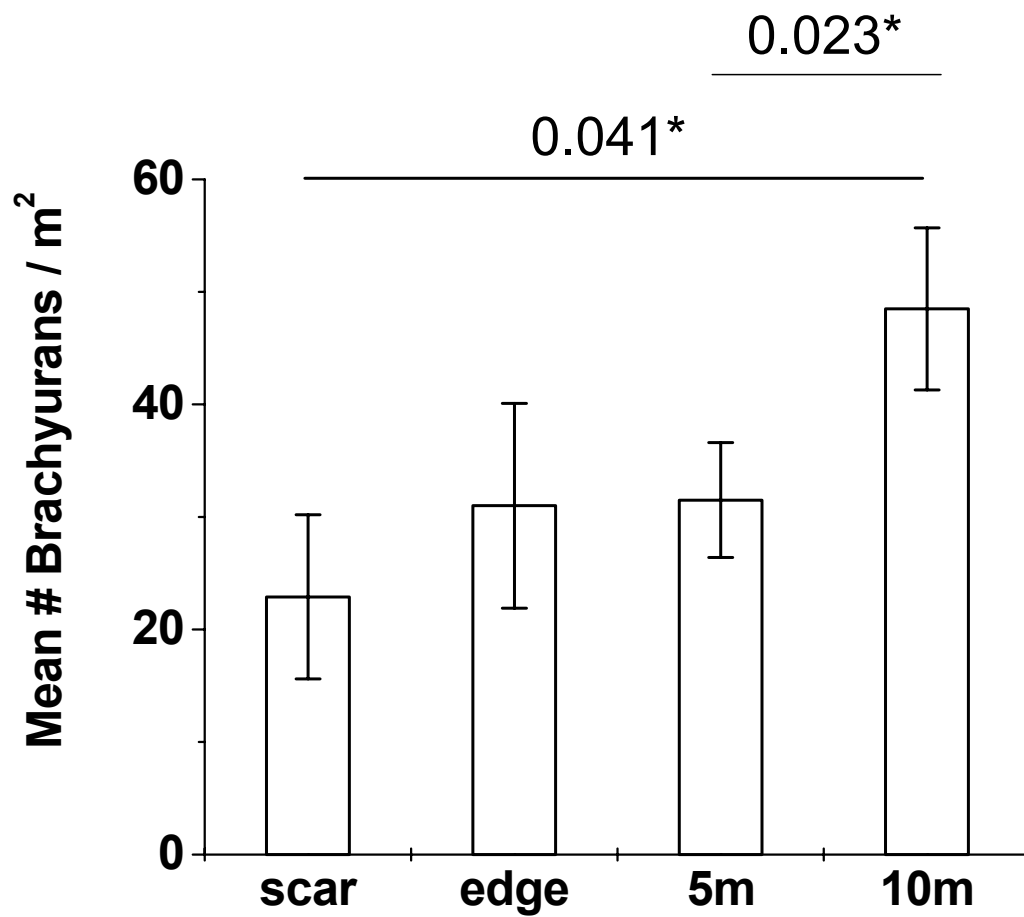


Figure 35. Mean (S. E.) Brachyuran abundance (# per m²) across all treatments. *significant at the per-contrast error rate (alpha = 0.05)

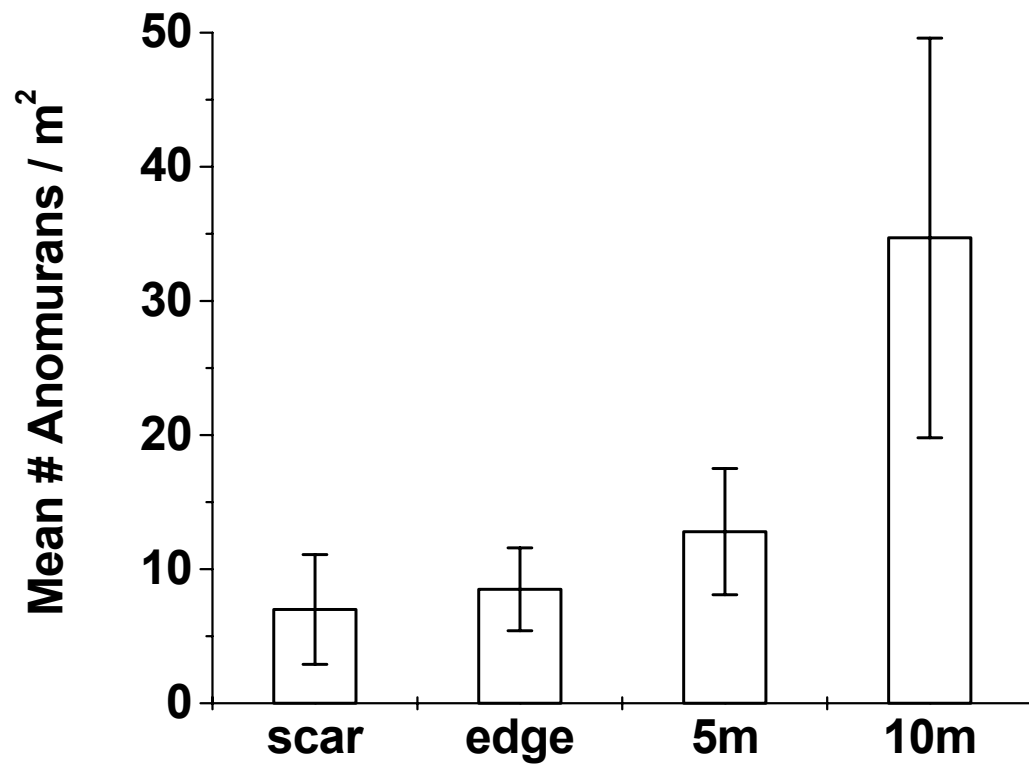


Figure 36. Mean (S. E.) Anomuran abundance (# per m²) across all treatments (N = 10). No contrasts were significant.

Table 14. Number and percent composition of molluscs collected across all treatments.

Mollusc Taxon	# Individuals	Percent
<i>Cerithium eberneum</i>	147	32.0
<i>Cerithiopsis greeni</i>	48	10.4
<i>Modulus modulus</i>	44	9.6
<i>Tricolia bella</i>	40	8.7
<i>Tegula fasciata</i>	27	5.9
<i>Acmaea</i> sp.	22	4.8
<i>Anachis pulchella</i>	19	4.1
<i>Nassarius albus</i>	17	3.7
<i>Turbo castanea</i>	16	3.5
<i>Ischnochiton</i> sp.	14	3.0
<i>Smaragdia viridis</i>	14	3.0
<i>Arene tricarinata</i>	10	2.2
<i>Bulla striata</i>	7	1.5
<i>Acanthochitona pygmaea</i>	6	1.3
<i>Crepidula convexa</i>	5	1.1
<i>Crassinella guadalupensis</i>	4	0.9
<i>Diodora</i> sp.	2	0.4
<i>Cerithium litteratum</i>	2	0.4
<i>Columbella mercatoria</i>	2	0.4

Table 14. Con't.

Mollusc Taxon	# Individuals	Percent
<i>Engoniophos unicinctus</i>	2	0.4
<i>Olivella floralia</i>	2	0.4
<i>Fissurella</i> sp.	1	0.2
<i>Brachiodontus exustus</i>	1	0.2
F. Columbellidae	1	0.2
F. Turridae	1	0.2
<i>Antillophos</i> sp.	1	0.2
<i>Arene</i> sp.	1	0.2
<i>Astraea phoebia</i>	1	0.2
<i>Conus jaspides</i>	1	0.2
<i>Cerithiopsis emersoni</i>	1	0.2
<i>Leucozonia</i> sp.	1	0.2
Total Molluscs	460	

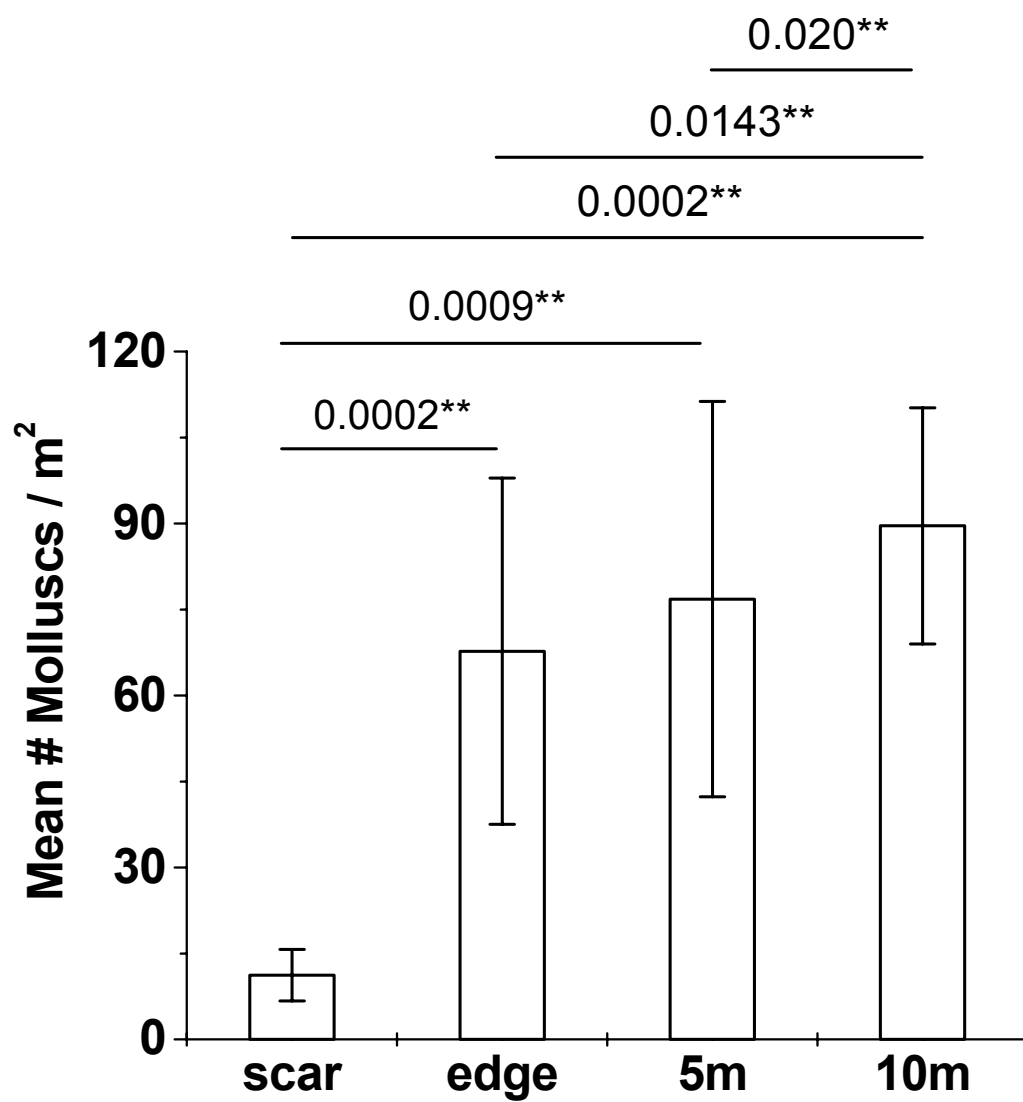


Figure 37. Mean (S. E.) mollusc abundance (# per m²) across all treatments (N = 10). **significant after correcting for multiple comparisons

Table 15. Mean (S. E.) number of molluscs per m² within each treatment (N = 10).

Mollusc Taxon	scar	edge	5 m	10 m
<i>Cerithium eberneum</i>	4.8 (3.2)	22.9 (16.1)	24.1 (14.2)	26.6 (13.5)
<i>Cerithiopsis greeni</i>	0 (0)	7.5 (2.3)	11.7 (9.5)	6.4 (2.5)
<i>Modulus modulus</i>	1.1 (0.7)	5.3 (2.5)	6.4 (3.5)	10.7 (3.0)
<i>Tricolia bella</i>	0.5 (0.5)	4.8 (1.5)	8.5 (4.6)	7.5 (2.3)
Pooled Molluscs [†]	4.8 (1.9)	27.2 (10.7)	26.1 (5.9)	38.4 (6.6)
Total Molluscs	11.2 (4.1)	67.7 (30.2)	76.8 (34.5)	89.6 (20.6)

[†]includes:

<i>Tegula fasciata</i>	<i>Columbella mercatoria</i>
<i>Acmaea</i> sp.	<i>Engoniophos uncinatus</i>
<i>Anachis pulchella</i>	<i>Olivella floralia</i>
<i>Nassarius albus</i>	<i>Fissurella</i> sp.
<i>Turbo castanea</i>	<i>Brachiodontus exustus</i>
<i>Ischnochiton</i> sp.	F. Columbellidae
<i>Smaragdia viridis</i>	F. Turridae
<i>Arene tricarinata</i>	<i>Antillophos</i> sp.
<i>Bulla striata</i>	<i>Arene</i> sp.
<i>Acanthochitona pygmaea</i>	<i>Astraea phoebia</i>
<i>Crepidula convexa</i>	<i>Conus jaspideus</i>
<i>Crassinella guadalupensis</i>	<i>Cerithiopsis emersoni</i>
<i>Diodora</i> sp.	<i>Leucozonia</i> sp.
<i>Cerithium litteratum</i>	

Table 16. P-values resulting from paired, two-tailed t-tests comparing differences in mean number of molluscs per m² between pairs of treatments.

*significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons; N/A = insufficient data to run analysis

Mollusc Taxon	scar-- edge	scar-- 5 m	scar-- 10 m	edge-- 5 m	edge-- 10 m	5 m-- 10 m
<i>Cerithium eberneum</i>	0.109	0.197	0.031*	0.866	0.360	0.132
<i>Cerithiopsis greeni</i>	N/A	N/A	N/A	0.169	0.280	0.408
<i>Modulus modulus</i>	0.094	0.295	0.002**	0.586	0.094	0.057
<i>Tricolia bella</i>	0.006**	0.016*	0.003**	0.857	0.558	0.663
Pooled Molluscs [†]	0.0008**	0.001**	0.0009**	0.409	0.078	0.034*
Total Molluscs	0.0002**	0.0009**	0.0002**	0.691	0.014**	0.020**

[†]includes:

Tegula fasciata
Acmaea sp.
Anachis pulchella
Nassarius albus
Turbo castanea
Ischnochiton sp.
Smaragdia viridis
Arene tricarinata
Bulla striata
Acanthochitona pygmaea
Crepidula convexa
Crassinella guadalupensis
Diodora sp.
Cerithium litteratum

Columbella mercatoria
Engoniophos unicinctus
Olivella floralia
Fissurella sp.
Brachiodontus exustus
F. Columbellidae
F. Turridae
Antillophos sp.
Arene sp.
Astraea phoebia
Conus jaspides
Cerithiopsis emersoni
Leucozonia sp.

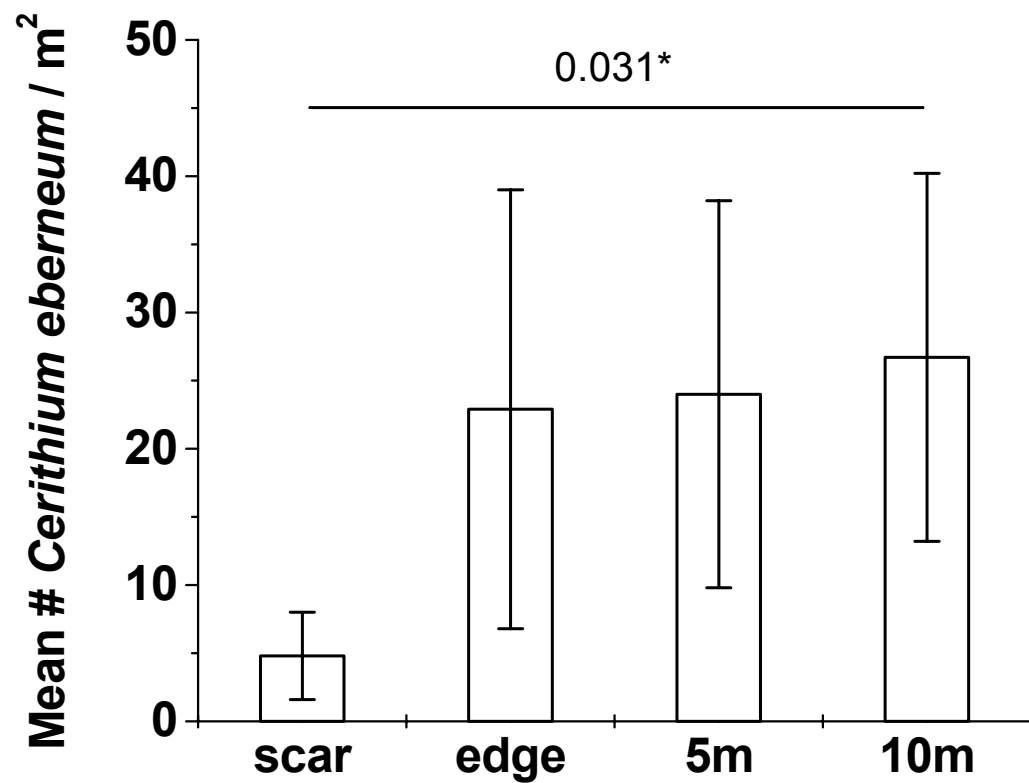


Figure 38. Mean (S. E.) *Cerithium eberneum* abundance (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05)

different for *Cerithium eberneum* (Table 16, Figure 38). No individuals of *Cerithiopsis greeni* were collected from scar habitat, versus an average of 25.6 individuals per m² in the other three treatments (Table 15, Figure 39). Although direct testing was not possible, by definition, all comparisons involving the scar treatment were significant. *Modulus modulus*, the third most abundant mollusc, had significantly lower densities in scars when compared to the 10 m treatment (Table 16, Figure 40). Finally, *Tricolia bella* densities were significantly lower in the scar versus all other treatments (Table 16, Figure 41).

The remaining 26 species accounted for 39.0 % of the total molluscs (Table 14). Pooled mollusc densities ranged from 4.8 individuals per m² in the scar to 38.4 individuals per m² in the 10 m treatment (Table 15). Scar densities of pooled molluscs were significantly lower than densities in the other treatments, and densities in the 5 m treatment were significantly lower than densities in the 10 m treatment (Table 16, Figure 42).

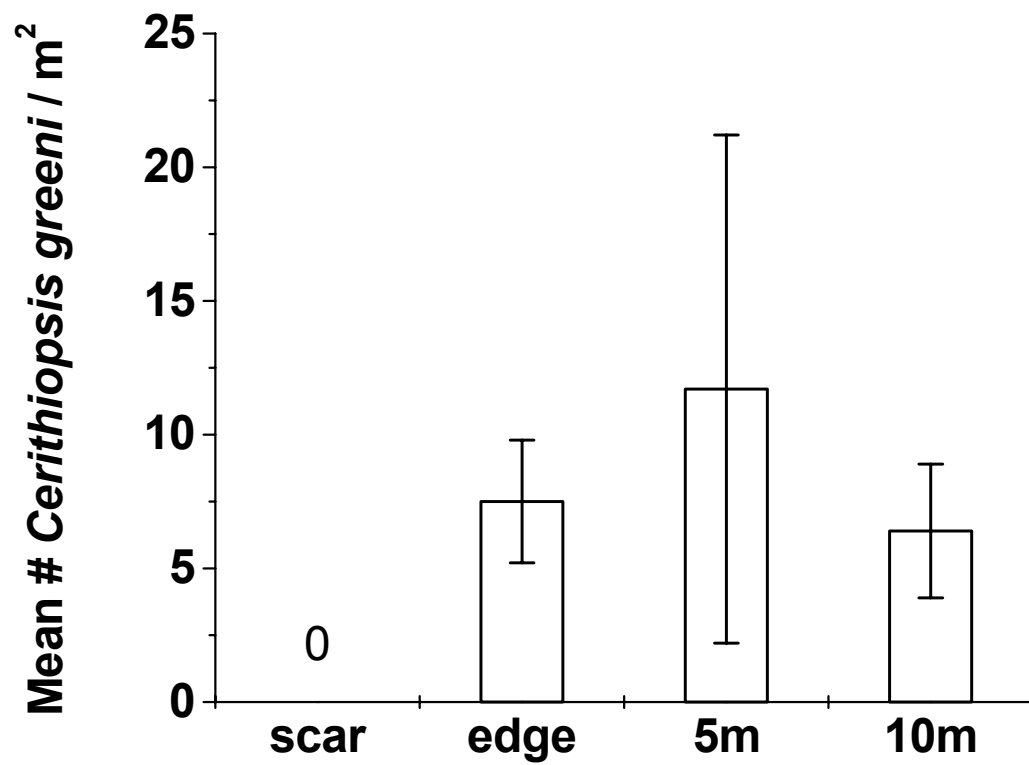


Figure 39. Mean (S. E.) *Cerithiopsis greeni* abundance (# per m²) across all treatments (N = 10).

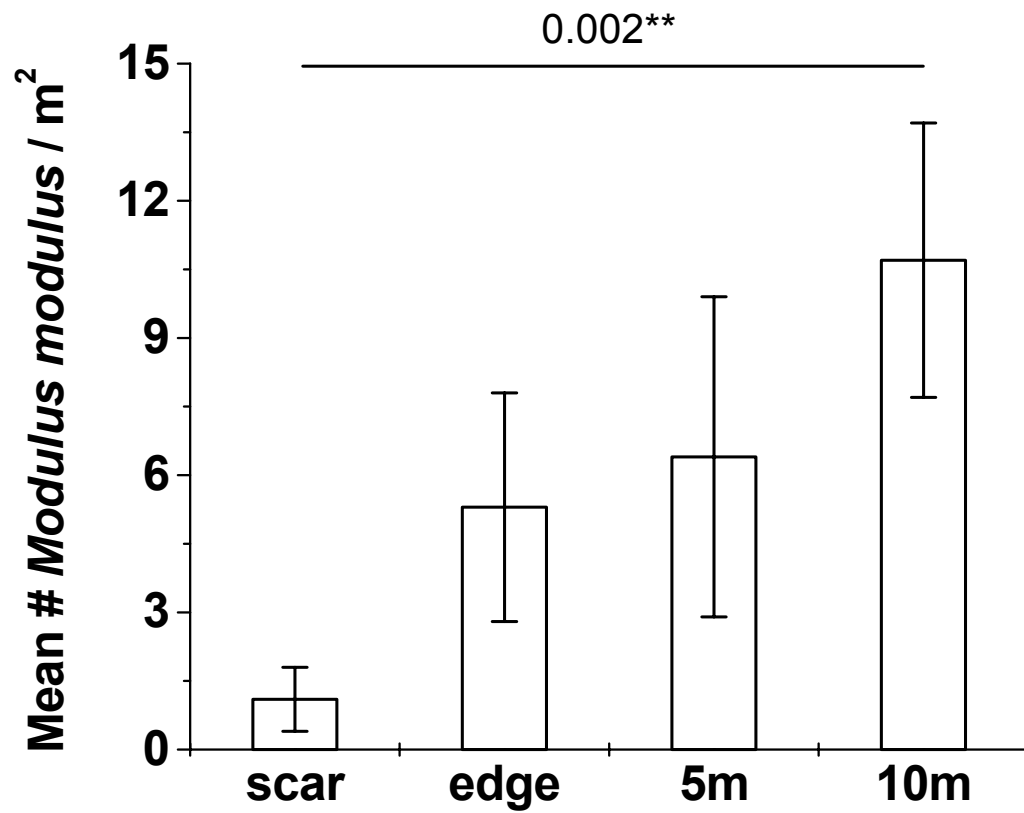


Figure 40. Mean (S. E.) *Modulus modulus* abundance (# per m²) across all treatments (N = 10). **significant after correcting for multiple comparisons

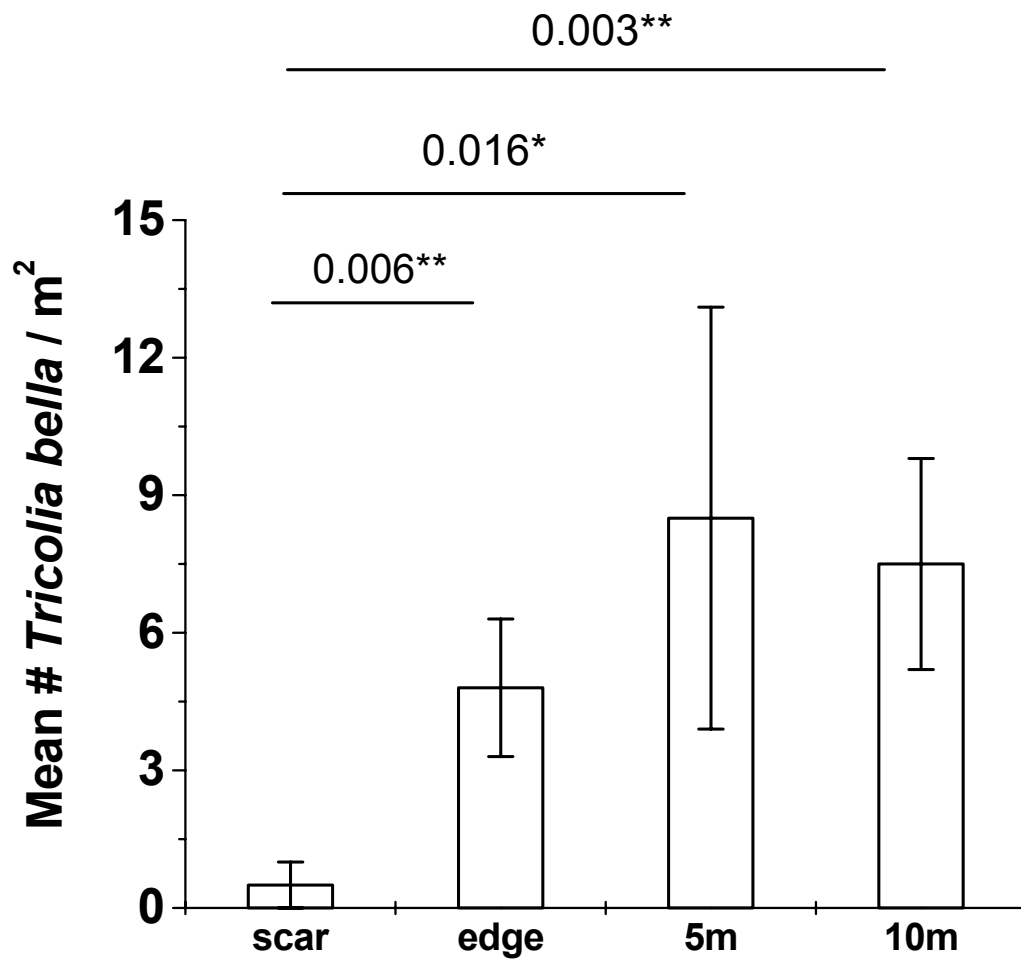


Figure 41. Mean (S. E.) *Tricolia bella* abundance (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons

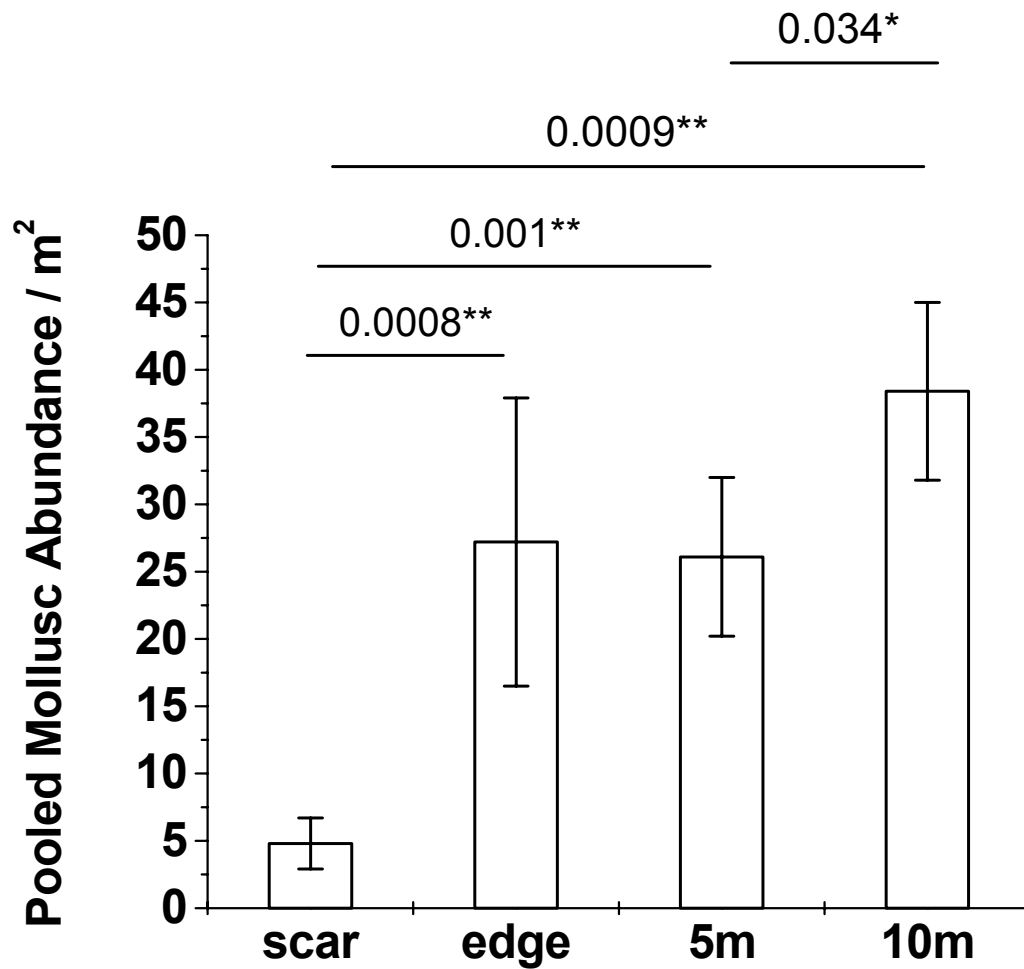


Figure 42. Mean (S. E.) abundance of pooled molluscs (# per m²) across all treatments (N = 10). *significant at the per-contrast error rate (alpha = 0.05); **significant after correcting for multiple comparisons

4. DISCUSSION

Just as naturally occurring sand substrates contain fewer total fauna and fewer species than adjacent vegetated areas, so do bare sand gaps created by propeller scarring (but see Young and Young, 1982). These differences are reflected in certain faunal groups as well. Shrimps and molluscs, more often directly associated with seagrass blades, exhibit significantly reduced abundances in propeller scars. Propeller scarring removes seagrass blades, the preferred habitat of these organisms, and thus fewer individuals of these taxa are found in scars. Additionally, my data suggest that scars act as barriers for lower mobility taxa such as shrimps and molluscs. In contrast, for more mobile fauna, scars do not present a significant boundary to movement. Highly mobile species may be less sensitive to boundaries and patch configuration (Wiens et al., 1985; Kotliar and Wiens, 1990; Wiens, 1992) which appears to be the case for some seagrass fauna (Holmquist, 1998). The relatively mobile fishes in this study may not have responded to scars as unsuitable habitat, perhaps as a result of the small scale of these gaps. Some studies have found similar patterns for naturally occurring sand substrates versus vegetated areas (Hanekom and Baird, 1984; Heck and Thoman, 1984; Bell and Westoby, 1986; Connolly, 1994b) which are contrary to the majority of studies that have examined seagrass fish distributions (Sogard et al., 1987; Bell and Pollard, 1989; Sogard and Able, 1991; Connolly, 1994a; Edgar and Shaw, 1995).

Although faunal communities in scars and the surrounding seagrass include similar taxa, scarring can modify species dominance for certain

numerically abundant taxa. For example, shrimp species known to utilize the blades of seagrass plants, such as *Thor manningi* and *Hippolyte zostericola* / *pleuracanthus*, dominated seagrass edge and interior treatments but showed significantly decreased abundances in scars. In the scars, *Alpheus normanni* and *Trachypenaeus* sp., often associated with bare sand patches (Holmquist, 1992), were the most abundant shrimps.

Although propeller scarring had no effect on species richness in the surrounding seagrass, there was a negative response for total fauna abundance, and the abundances of crabs and molluscs, up to a distance of 5 m from scars. Similar declines have been reported from edges of fragmented forests (Ozanne et al., 1997; Stevens and Husband, 1998). Stevens and Husband (1998) observed decreased numbers of small mammal species at edges of forest fragments in the Brazilian Atlantic forest, with declines penetrating up to 160 m for some taxa. In a temperate forest of Buckinghamshire, Great Britain, Ozanne et al. (1997) found significantly decreased arthropod densities at fragmented forest edges, which extended 25 m into the forest for some taxa. The authors attribute these declines to microclimate variation and increased predation pressure at edges (Ozanne et al., 1997; Stevens and Husband, 1998). In addition, vegetation structure at fragmented forest edges differs from that of the interior which may play a role in structuring faunal communities (Lovejoy et al., 1986; Williams-Linera, 1990).

Faunal species numbers and abundances increase with increasing seagrass biomass and density, suggesting that faunal abundance may reflect

changes in seagrass structure (Orth, 1973, 1977; Heck and Wetstone, 1977; Brook, 1978; Heck and Orth, 1980; Stoner, 1980a, 1980b, 1983b; Lewis, 1984; Stoner and Lewis, 1985; Bell and Westoby, 1986). However, in the present study, seagrass density and biomass at edges did not differ from seagrass at 5 m and 10 m distance. Dawes et al. (1997) also found no significant differences in number of *T. testudinum* short shoots (in addition to blade morphology and productivity) between seagrass fringing a propeller scar and seagrass located 1-2 m from a scar. These findings are contrary to studies of natural seagrass bed edges where peripheral plant density and biomass are lower than bed interiors (Zieman, 1972; Orth, 1977; Thayer and Fonseca, 1984; Duarte and Sand-Jensen, 1990; Bologna, 1998; Nakaoka and Aioi, 1999) and do not support the argument that faunal distributions reflect seagrass structural differences.

Fine sediments are known to accumulate in the interior portions of seagrass beds (Scoffin, 1970; Orth, 1977; Almasi et al., 1987). Interestingly, the seagrass interior treatments in the present study did not show increased percentages of fines relative to the other treatments. Similar results are reported from Tampa Bay, Florida grass beds where sediment particle sizes did not differ significantly between seagrass fringing a scar and seagrass at some distance from the scar (Dawes et al., 1997). Finer sediments may be immediately blown from the scar upon the initial cut of the propeller, leaving behind higher proportions of gravel versus the surrounding seagrass as seen in the present study. Additionally, fines may be more easily eroded from scars without the sediment trapping effect of seagrass.

The presence of bare patches (i.e. propeller scars) within a continuous seagrass meadow alters the velocity of water moving across the meadow (Fonseca, pers. comm). The increased water motion observed at the immediate edges of scars is consistent with previous research on seagrass flow dynamics (Fonseca et al., 1983). Water velocity decreases as the scar is passed over, increases at the immediate scar/seagrass edge, and decreases progressively as the water moves through continuous grass and is dampened (Fonseca et al., 1983; Fonseca, pers. comm.).

Changes in predation rates at edges may play a part in structuring the distribution of crabs and molluscs. Increased edge associated with forest fragmentation has been implicated in high bird nest predation rates (Andrén et al., 1985; Andrén, 1992). In the marine environment, high rates of predation on juvenile scallops were observed in very patchy seagrass (increased edges) in North Carolina (Irlandi et al., 1995). Additionally, increased numbers of predatory fishes were found at salt marsh edges, (Peterson and Turner, 1994; Kneib, 2000) and these predators utilized unvegetated channels in the marsh as alley ways. Perhaps a similar activity occurs in propeller scars, with larger predatory fishes utilizing scars as alleys, with quick forays into the fringing seagrass to feed. Larger fishes, such as snapper, were observed in scars, especially scars with exposed rhizomes at the margins (pers. obs.).

The results of my study have direct applicability to issues raised regarding the assessment of seagrass injuries. My results show that ecological changes resulting from propeller scarring are not limited to the footprint of the scar, but

can extend some distance away from the scar depending upon the faunal taxa under consideration. At a distance of 5 m from a single propeller scar, crab and mollusc densities are negatively affected. In areas with multiple scarring, there is the potential for these sensitive taxa to be driven out if the distance between scars is less than 5 m. When considering restoration of damaged beds to pre-injury conditions, the distributions of fauna in comparable undisturbed areas must first be established. Secondly, it must be determined which species are impacted negatively and to what extent. Restoration efforts should then seek to ameliorate these effects by restoring damaged areas in such a way that the amount of optimal habitat is maximized (i.e. pre-injury distributions can be maintained).

This study addresses issues pertaining to single propeller scar disturbances. In contrast, when areas become riddled with scars, there is proportionally less seagrass coverage, biomass, and productivity and more edge habitat. Bed edges erode, leading to increased sediment suspension, and current flow can be radically altered (Walker et al., 1989; Fonseca, 1996). Given that current patterns and velocities have the potential to shape seagrass beds (Fonseca et al., 1983), continual scarring may further degrade and restructure the bed, leading to fragmentation of a once continuous meadow (Walker et al., 1989). Long-term bed persistence and physical integrity are jeopardized. Future research should include the examination of distributions of a wider variety of species in more heavily scarred areas at larger spatial and longer time scales.

5. LITERATURE CITED

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